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The Great Basin Naturalist

VOLUME 35, 1975

Editor: Stephen L. Wood

THE GREAT BASIN NATURALIST
BYU PROVO, UTAH
1939

Published at Brigham Young University, by
Brigham Young University

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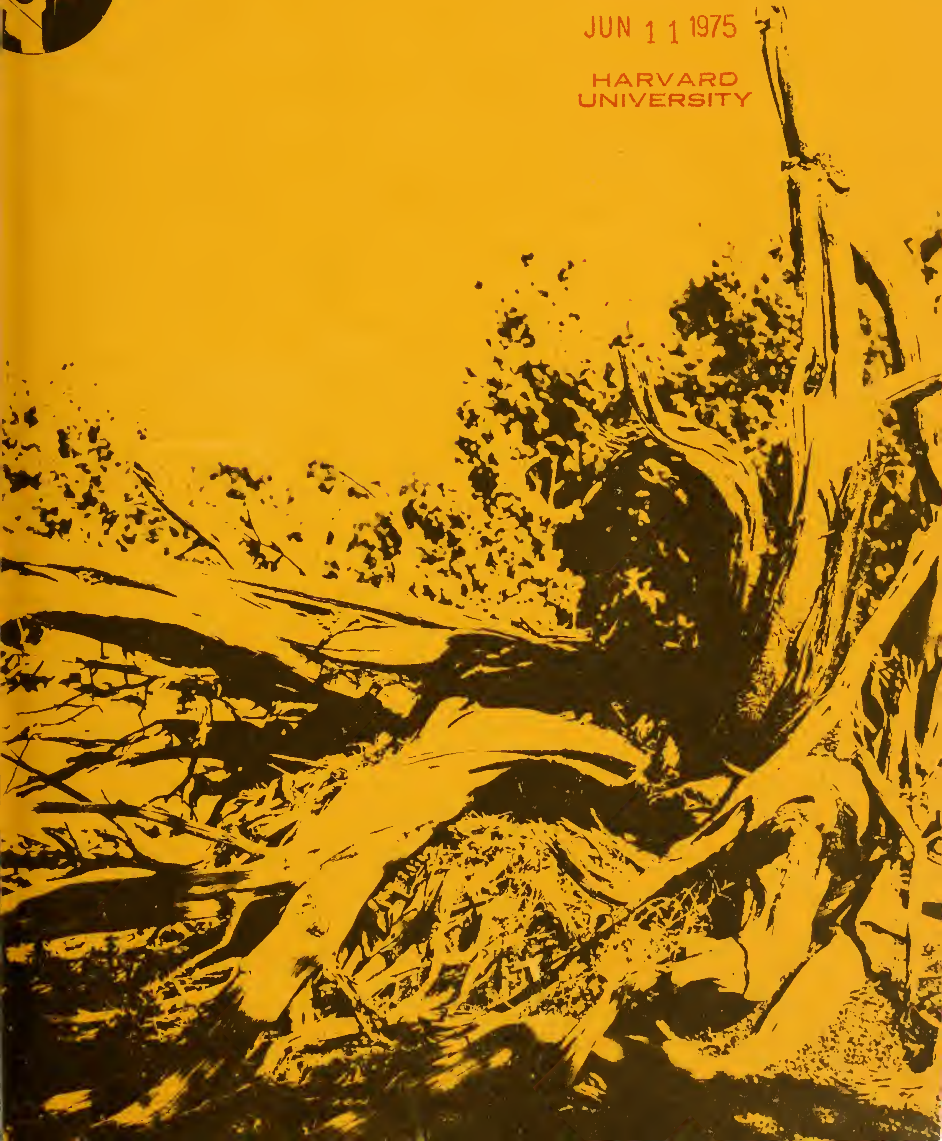

GREAT BASIN NATURALIST

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Subscriptions. The annual subscription is $9 (outside the United States $10). The price for single numbers is $3 each. All back numbers are in print and are available for sale. All matters pertaining to the purchase of subscriptions and back numbers should be directed to Brigham Young University Press, Marketing Department, 204 UPB, Provo, Utah 84602.

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Manuscripts. All manuscripts and other copy for the *Great Basin Naturalist* should be addressed to the editor as instructed on the back cover.

The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

VOLUME 35 March 31, 1975 No. 1

EVOLUTION OF THE SCELOPORINE LIZARDS (IGUANIDAE)

Kenneth R. Larsen[1] and Wilmer W. Tanner[2]

ABSTRACT.— Phylogenetic relationships among Sceloporine genera are briefly discussed. Species relationships within the genus *Sceloporus* are analyzed, and evolutionary lines of descent are proposed.

The genus *Sceloporus* is composed of three monophyletic groups: Group I, the most primitive, probably developed from *Sator*-like ancestral stock in Miocene times. This group speciated from stock similar to *Sceloporus gadoviae* in southern Mexico to *S. merriami* in the North and contains 7 species in 3 species groups. We propose that these species be included in the genus *Lysoptychus* Cope. Group II arose from Group I and evolved from centrally located *Sceloporus pictus* in all directions throughout Mexico. This intermediate group contains approximately 19 species in 5 species groups. Group III also arose from the primitive stock of Group I and radiated from several desert refugia created by Pleistocene glaciation. Evolution of this group in Mexico was generally from north to south with *Sceloporus malachiticus* extending as far south as Panama. This group contains approximately 33 species in 5 species groups.

In a previous paper (Larsen and Tanner, 1974) we presented our analysis of the species in the lizard genus *Sceloporus*. Numerical statistical methods were used to analyze the species in the genus *Sceloporus* using cranial osteology, external meristic and numeric characters, karyology, display behavior, and geographic distribution. A new classification for the genus was proposed with three major branches or groups. Group I contained 7 species in 3 species groups. Group II contained approximately 19 species in 5 species groups. Group III contained approximately 33 species in 5 species groups. This classification was supported by the cluster analysis of several different sets of data. Cranial osteology, zoogeography, behavior, and karyology were shown to be taxonomically significant as numeric characters. Stepwise discriminate analysis showed that this classification of the species of *Sceloporus* into 3 major groups and 13 species groups was significant at the .999 confidence level.

The purpose of this paper is to present our views on the evolution of the species in the genus *Sceloporus*. We also propose a phylogeny of closely related (Sceloporine) genera. We are grateful for the assistance of H. M. Smith, C. C. Carpenter, W. P. Hall, and the following persons at Brigham Young University: A. L. Allen, F. L. Anderson, J. R. Murphy, M. S. Peterson, J. K. Rigby, N. M. Smith, D. A. White, and S. L. Wood.

INTERGENERIC PHYLOGENY

In 1828 Weigmann described several genera, including *Sceloporus* (*S. torquatus*). He distinguished *Sceloporus* from the South American *Tropidurus* mainly on the basis of femoral pores (*Scelo*=thigh, *porus*=pore). In 1852 Baird and Girard described the genus *Uta* (*U. stansburiana*) which is distinguished from the smaller species of *Sceloporus* by its gular fold and granular dorsal scales. In 1854 Hallowell erected the genus *Urosaurus* (*U. graciosus*), which is similar to *Uta* but has several rows of enlarged, carinate, imbricate vertebrals or paravertebrals. Two years later Duméril (1856) described the genus *Phymatolepis* (*Urosaurus bicarinatus*) on the basis of enlarged paravertebrals. In 1859 Baird placed Hallowell's genus *Urosaurus* in synonymy with *Uta*, and in

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1864 Cope did the same with Duméril's *Phymatolepis*. Boulenger (1885) raised Cope's *Uta thalassina* to generic status (*Petrosaurus*), but Cope (1900) rejected this proposal and made *Petrosaurus* a third synonym of *Uta*. In 1888 Cope erected the genus *Lysoptychus* (*L. lateralus*= *Sceloporus couchi*) on the basis of a single specimen that appeared to have a well-developed gular fold. Subsequent investigation (Stejneger, 1904) showed the "gular fold" to be an artifact of preparation on a single specimen which "was preserved in such a manner as to make a fold across the neck, which formed the basis for the erection of the genus" (Smith, 1939, p. 242). Dickerson (1919) described the genus *Sator* (*S. grandaevus*) which has persisted despite *Sator's* close similarity to *Uta*, *Urosaurus* and *Sceloporus*. In 1942 Mittleman resurrected the genera *Urosaurus* and *Petrosaurus*. He also erected the genus *Streptosaurus* based on *Uta mearnsi*, which is most similar to *Petrosaurus*. He proposed that *Uta*, *Urosaurus*, and *Sator* all arose independently from *Sceloporus*. He placed *Phrynosoma* with the above genera in a distinct group. Smith (1946) moved *Sauromalus* and *Dipsosaurus* to more primitive positions but otherwise retained Mittleman's arrangement. Savage (1958) placed *Streptosaurus* in synonymy with *Petrosaurus*. He separated *Uta* from *Urosaurus* mainly on the basis of sternal and costal morphology. He placed *Uta* and *Petrosaurus* with the sand lizards (*Holbrookia*, *Uma*, and *Callisaurus*), leaving *Sceloporus*, *Sator*, and *Urosaurus* together. Etheridge (1964) rejected Savage's wide separation of *Uta* and *Urosaurus*, and placed *Uta*, *Urosaurus*, *Sator*, and *Sceloporus* on one side and *Uma*, *Holbrookia*, and *Callisaurus* on the other. Primitive to both groups was *Petrosaurus*. A sand lizard resurrected by Clarke (1965) was Troschel's (1852) genus *Cophosaurus* (*C. texanus*, previously *Holbrookia texana*).

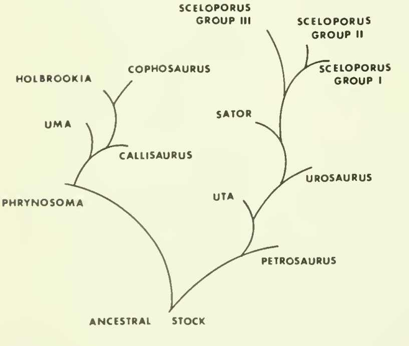

Fig. 1. Phylogeny of sceloporine genera and the three major groups in *Sceloporus*.

Presch (1969) rejected Etheridge's removal of *Phrynosoma* from the sceloporines and placed *Phrynosoma* with the sand lizards as a primitive member of that group. On the basis of scleral ossicles, Presch (1970) indicated that *Petrosaurus* is a primitive member of the *Sceloporus* branch. Ballinger and Tinkle (1972) proposed an early separation of the *Uta* and *Petrosaurus* stock from the ancestor of *Urosaurus*, *Sator*, and *Sceloporus*.

Several characters suggest further modification of the above arrangement. Our proposed phylogeny of sceloporine genera is illustrated in Figure 1. *Urosaurus* shows a tendency for enlarged scales near the midline of the dorsum. This trend is further developed in *Sator*, which has enlarged dorsals and granular laterals. The migration of enlarged scales around the sides of the body and the increase in scale size and degree of imbrication, mucronation, and carination is a general trend along the chain of genera from *Petrosaurus* to *Sceloporus*. The new phylogeny is also supported by the gradual decrease in development of the gular fold, which is completely lost in all species of *Sceloporus* in Group III. Most of the species in Group I have what Smith (1939) called a rudimentary gular fold. Some of the species in Group II show a less pronounced tendency to develop a gular fold, and Group III lacks it completely. The gradual loss of the gular fold in the *Sceloporus* complex is more probable than a loss (from *Petrosaurus* to *Sceloporus*) and subsequent redevelopment (from *Sceloporus* to *Uta*, *Urosaurus*, or *Sator*). This reversal of the phylogeny resolves a question raised by Smith (1946:178): "It is a curious fact that all genera that have sprung from *Sceloporus* have developed a gular fold—including *Sator*, a Baja California genus. The tendency to develop this fold appears to be restricted to the primitive groups of *Sceloporus* . . . and these are the groups from which *Uta*, *Urosaurus*, and *Sator* independently appear to have been derived."

Although Smith pointed to this problem, he nevertheless accepted Mittleman's arrangement of the sceloporine genera. More recently, Smith (per comm.): has agreed that *Sceloporus* may be derived with respect to *Uta, Urosaurus*, and *Sator*. This position has also been suggested by Hall (pers. comm.): "Inspection of the structure of the femoral pores and their surrounding scales, and the development of mucronation and carination of the body scales, to mention but two sets of characters in various primitive *Sceloporus* and in other sceloporine genera, will suggest that *Sceloporus* is derived even in respect to *Uta* and *Urosaurus*."

We suggest the following conclusions with regard to the new phylogeny and published data on hip ratios of displaying males (Purdue and Carpenter, 1972a, 1972b). The hip ratio (vertical hip movement to vertical eye movement) increased from *Petrosaurus* (0.68) to *Uta* (average 0.74) to *Urosaurus* (average 1.06). After the transition from *Sator* (no published data on hip ratios) to *Sceloporus*, the trend reversed and hip ratios decreased from an average of 1.21 in Group I to 0.66 in Group II to 0.34 in Group III (averages computed from Purdue and Carpenter, 1972b).

Etheridge (1964) illustrated clavicles and scapulocoracoids of 8 sceloporine genera (excluding *Phrynosoma*). If his drawings are superimposed on the new phylogeny (Fig. 2), two trends are apparent: (1) a gradual development of the scapular fenestra (top groove) from *Petrosaurus* to *Sceloporus* Group III, and (2) an increase in size of the clavicular hook. If *Urosaurus* and *Uta* were derived from *Sceloporus*, the scapular fenestra would have developed and then disappeared from *Petrosaurus* to *Sceloporus* to *Uta*. This improbable reversal is similar to the problem with the gular fold. We are persuaded that the new phylogeny is more probable.

Intrageneric Phylogeny

The first phylogenetic schemes for the genus *Sceloporus* were proposed by Smith (1934, 1937a, 1937b, 1938, 1939). Other workers have recently modified the phylogeny on the basis of karyology (Cole, 1970, 1971a, 1971b; Hall, 1971, 1973), and behavior (Bussjaeger, 1971).

Larsen and Tanner (1974) redefined relationships among the species in the genus *Sceloporus*. We used Ward's cluster analysis (Wishart, 1968) to cluster 55 species on the basis of external characters, cranial osteology, karyology, behavior, and zoogeography (Fig. 3). We then used step-wise discriminate analysis (Dixon 1967) and found that the arrangement of groups and subgroups is significant at the .999 level of confidence (Table 1).

Although Ward's cluster analysis provides a phenetic dendogram, it does not give any indication as to which branch of a cluster is derived and which is primitive. In 1939 Smith said, "The most primitive form of this group is undoubtedly *lunaei* which is closely related to *formosus malachiticus*" (p. 60). In other words, *lunaei* is the most primitive form

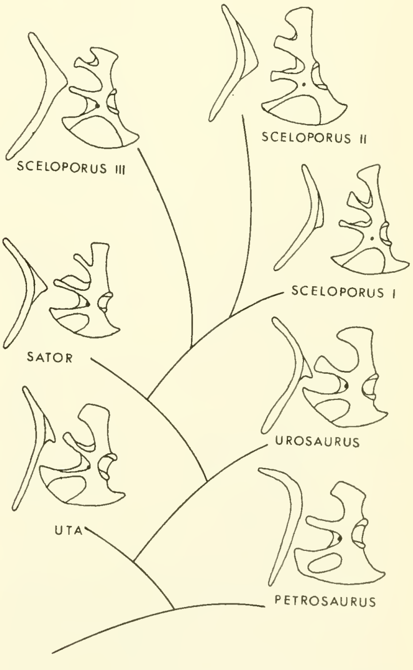

Fig. 2. Clavicles and scapulocoracoids of several sceloporines. All illustrations except *Sceloporus* I, *Sceloporus* II, and *Sceloporus* III are from Etheridge (1964).

TABLE 1.—Groups and subgroups in the genus *Sceloporus*

Group I (7 spp.)	Group II (20 spp.)	Group III (33 spp.)
Subgroup A (1 spp.)	Subgroup A (7 spp.)	Subgroup A (9 spp.)
gadoviae	grammicus	spinosus
Subgroup B (2 spp.)	pictus	orcutti
couchi	megalepidurus	clarki
merriami	cryptus	melanorhinus
Subgroup C (4 spp.)	shannonorum*	magister
maculosus	heterolepis	olivaceus
parvus	asper	cautus
jalapae	Subgroup B (2 spp.)	horridus
ochoterenae	pyrocephalus	edwardtaylori
	nelsoni	Subgroup B (7 spp.)
	Subgroup C (3 spp.)	formosus
	scalaris	lunaei
	goldmani*	malachiticus
	aeneus	acanthinus
	Subgroup D (4 spp.)	Subgroup C (5 spp.)
	siniferus	undulatus
	carinatus	virgatus
	utiformis	woodi
	squamosus	occidentalis
	Subgroup E (4 spp.)	graciosus
	variabilis	Subgroup D (4 spp.)
	cozumelae	jarrovi
	teapensis	lineolateralis
	chrysostictus	ornatus
		dugesi
		Subgroup E (8 spp.)
		torquatus
		cyanogenys
		bulleri
		insignis*
		macdougalli
		mucronatus
		serrifer
		poinsetti

*Species not examined in this study.

in the *spinosus* species group because it is most similar to a member of the next closest group (*formosus*). This statement by Smith is consistent with the following method of converting a phenetic dendrogram into a phylogeny (Fig. 4): If "A" is primitive to "B" it is less derived from (more similar to) the stem species "G." The more primitive member of the other cluster ("C" or "D") will also be more similar to "G." The more primitive members of the two clusters will therefore be phylogenetically "closer" and phenotypically more similar than any other combination from the two clusters. This rule can be applied objectively with a similarity matrix.

When all possible pairs between adjacent clusters are compared, the two most similar species are considered primitive within their respective clusters. This technique will convert a dendrogram into a phylogeny.

Ward's cluster analysis and the above phylogeny technique were repeated several times using external and osteological characters, distribution, karyology, behavior, and combinations of the above. (See Larsen and Tanner, 1974, for a presentation of results.) The differences among results were resolved subjectively to produce a composite phylogeny (Fig. 5). This procedure is based on several assumptions which are admittedly vulnerable. To restrict the scope of our study it was assumed that the alpha taxonomy is complete and correct. That is, it was assumed that all species of *Sceloporus* are now named and correctly defined in the literature. Of course, this assumption may be incorrect. But the purpose of our study is to produce a general overview and not a detailed taxonomic review. The details near the ends of branches are therefore tentative and subject to future review.

In spite of the large number of characters considered (over 80), these results are also subject to errors due to parallelism, convergence, varying rates of diver-

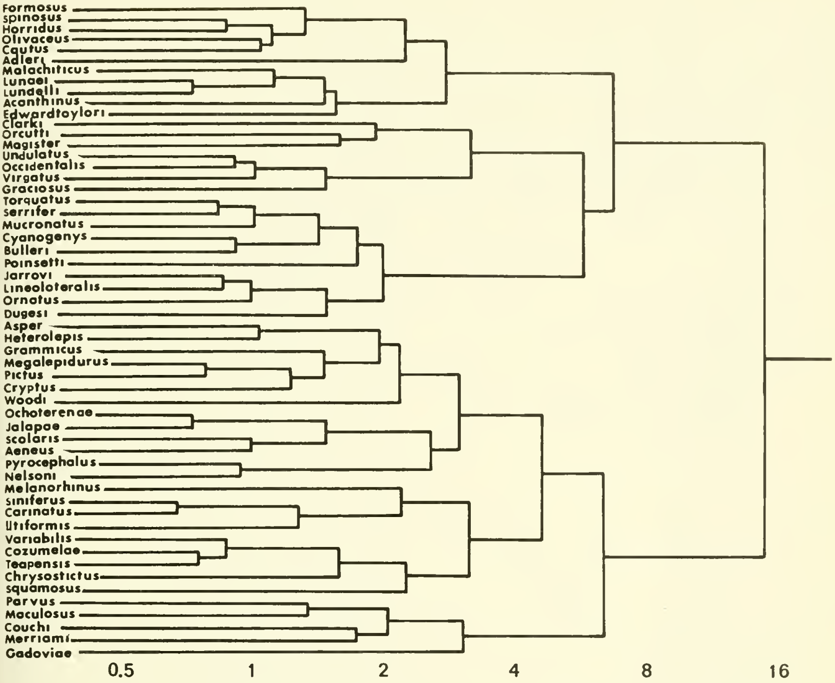
Formosus
spinosus
Horridus
Olivaceus
Cautus
Adleri
Malachiticus
Lunaei
Lundelli
Acanthinus
Edwardtaylori
Clarki
Orcutti
Magister
Undulatus
Occidentalis
Virgatus
Graciosus
Torquatus
serrifer
Mucronatus
Cyanogenys
Bulleri
Poinsetti
Jarrovi
Lineolateralis
Ornatus
Dugesi
Asper
Heterolepis
Grammicus
Megalepidurus
Pictus
Cryptus
Woodi
Ochoterenae
Jalapae
scalaris
Aeneus
pyrocephalus
Nelsoni
Melanorhinus
siniferus
Carinatus
Utiformis
Variabilis
Cozumelae
Teapensis
Chrysostictus
squamosus
Parvus
Maculosus
Couchi
Merriami
Gadoviae
0.5
1
2
4
8
16

Fig. 3. Dendrogram generated by Ward's cluster analysis of external, skull, and distribution characters (82 characters).

gence, pleiotrophy, and other cases in which the phenotype is not a direct manifestation of the genotype. All phylogenetic conclusions are subject to these limitations, and the systematist can do little more than acknowledge the circumstantial nature of his evidence.

We propose that *Sceloporus* is derived from *Uta* through *Urosaurus* and *Sator* (see above). Smith (1938) suggested that the connection between these genera is from *Urosaurus ornatus* to *Sceloporus couchi*. Smith included *couchi* in the *variabilis* species group.

Figure 6 shows the arrangement of species in Smith's *variabilis*, *maculosus*, and *merriami* groups according to Smith (1939, Fig. 42) and the new phylogeny. Four of these species (*couchi*, *parvus*, *maculosus*, and *merriami*) are transferred to Group I. Smith may have allowed for this by placing these four species on one side of his tree next to *Uta*. If *Uta* (*Uta*, *Urosaurus*, and *Sator*) is considered primitive to *Sceloporus*, then Smith's evidence supports our conclusion that Group I is primitive to the other two groups in *Sceloporus*. The remaining species in Smith's *variabilis* group (*variabilis*, *cozumelae*, and *teapensis*) are placed in Group II.

Smith (1939:239) allowed for the removal of *parvus* and *couchi* from the *variabilis* group with this statement:

> That *parvus* and *couchi* are only distantly related to the remainder of the group is shown by the widely different character of the ventral coloration in the males, smooth head scales, larger number of femoral pores, and general habitus. . . . It is my belief that this section approaches more closely the ancestral stock of *Uta* than the other species of the *variabilis* group.

Smith (p. 239) also associated *merriami* with *Uta*: "It would appear that *merriami* is closely related to *Uta*, and that *Uta*

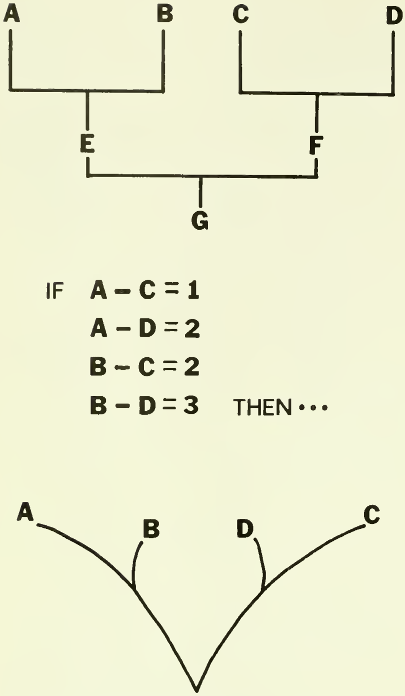

Fig. 4. Phylogeny theory. If the phenetic distance between "A" and "C" is less than that between any other pair, then "A" and "C" are primitive members in clusters "E" and "F."

arose from the forms now extinct which closed the present gap between *couchi* and *merriami*." Note that our new arrangement places *merriami* and *couchi* together.

Another divergence from Smith's phylogenetic tree is the addition of *chrysostictus* to the *variabilis* group. Smith (p. 239) supports this inclusion (and the close proximity of the *siniferus* group): "Another group closely related to the *variabilis* section is the *siniferus* series, which closely approaches the *variabilis* group through *cupreus*. . . . The *chrysostictus* group is also closely related."

Thus it can be seen that Smith allowed for the possibility of removing *parvus* and *couchi* and adding *chrysostictus*, which changes his *variabilis* group into the new *variabilis* group.

Smith stated that the *siniferus* group "closely approaches the *variabilis* group" and yet his illustration (1939, Fig. 3) has these groups separated by several other groups. In the new phylogeny they are adjacent.

Figure 7 compares Smith's arrangement of his *chrysostictus*, *utiformis* and *siniferus* groups with the new arrangement of the same species. Besides the placing of *chrysostictus* in the *variabilis* group (which has already been explained), the only major difference in Figure 4 is the removal of *ochoterenae* to place it in Group I. (The inclusion of *utiformis* in the *siniferus* group is minor). Smith listed 11 diagnostic characters of the *siniferus* group. In three cases he said "except *ochoterenae*" and in another "except *ochoterenae* and *cupreus*." He (p. 301) said, "Postanals tending to be poorly developed (except *ochoterenae* and *cupreus)*; two postrostrals (except *ochoterenae*, without postrostrals); . . . ventral scales pointed or, at least not notched (except *ochoterenae* in which they are notched) . . . males without distinctive ventral coloration (except *ochoterenae*)."

If size is discounted, then *ochoterenae* is different in 4 of the 10 diagnostic characters for the *siniferus* group. *S. ochoterenae* also has more femoral pores than any other species in Smith's *siniferus* group. Smith's conclusions, therefore, would not be seriously challenged if *ochoterenae* were removed from the *siniferus* group and placed in Group I next to *jalapae*. In fact, when describing *ochoterenae*, Smith (p. 309) said, "three or four scales on anterior border of ear, not so large as in *jalapae*." So apparently he was comparing these two species.

Smith included *jalapae* in his scalaris group, which is otherwise identical to the new *scalaris group* (Fig. 5). Removing *jalapae* from the *scalaris* group to place it in the primitive Group I is supported by the following statement by Smith (p. 331):

> The only species doubtfully included in this group is *jalapae*, which differs from the remaining forms in having lateral scales in distinctly oblique rows, and in lacking postrostrals [as does ochoterenae]. . . .
>
> *S. jalapae* is clearly the most primitive member of the group. *S. scalaris, aeneus* and *goldmani* are clearly more closely related to each other than any one of these is to *jalapae*.

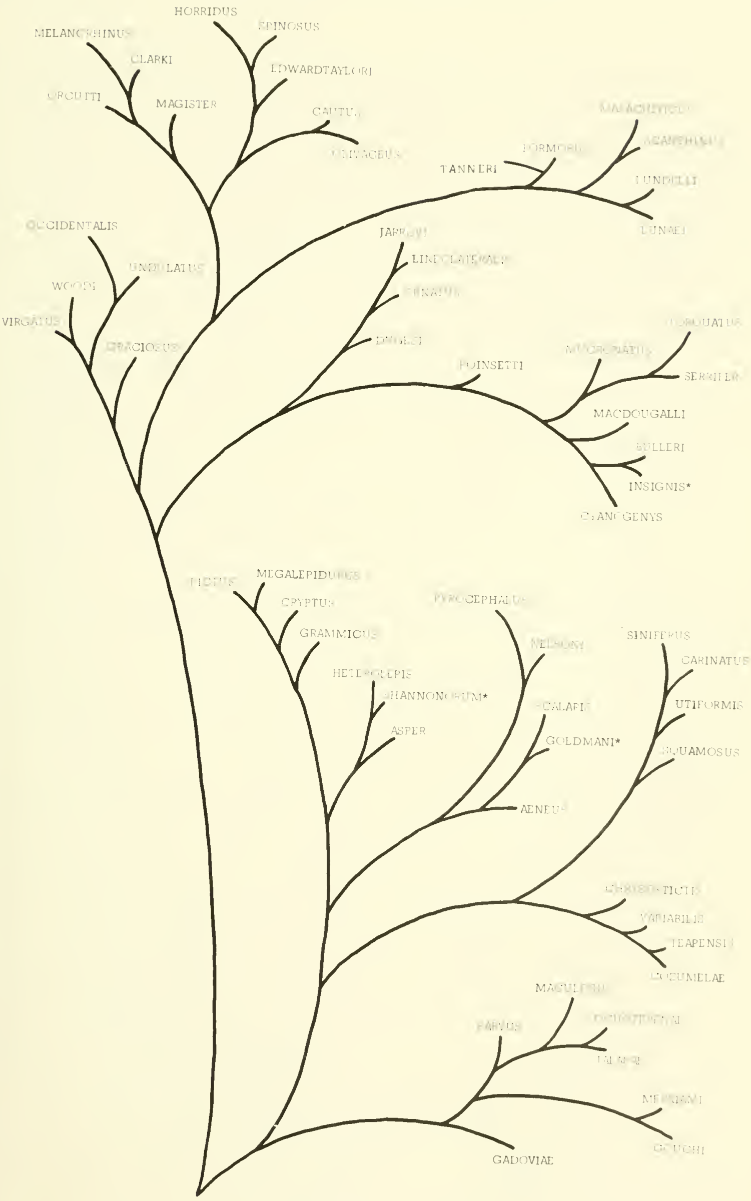
HORRIDUS
MELANORHINUS
SPINOSUS
CLARKI
EDWARDTAYLORI
ORCUTTI
MAGISTER
CAUTUS
OLIVACEUS
MALACHITICUS
FORMOSUS
ACANTHINUS
TANNERI
LUNDELLI
LUNAEI
OCCIDENTALIS
JARROVI
LINEOLATERALIS
UNDULATUS
WOODI
ORNATUS
VIRGATUS
DUGESI
GRACIOSUS
TORQUATUS
POINSETTI
MUCRONATUS
SERRIFER
MACDOUGALLI
BULLERI
INSIGNIS*
CYANOGENYS
MEGALEPIDURUS
NIGRIS
CRYPTUS
PYROCEPHALUS
GRAMMICUS
NELSONI
SINIFERUS
CARINATUS
HETEROLEPIS
SHANNONORUM*
JALAPAE
UTIFORMIS
ASPER
GOLDMANI*
SQUAMOSUS
AENEUS
CHRYSOSTICTUS
VARIABILIS
TEAPENSIS
COZUMELAE
MACULOSUS
PARVUS
[illegible]
[illegible]
MERRIAMI
COUCHI
GADOVIAE

Fig. 5. Proposed phylogeny for the genus *Sceloporus*. (* = species not examined.)

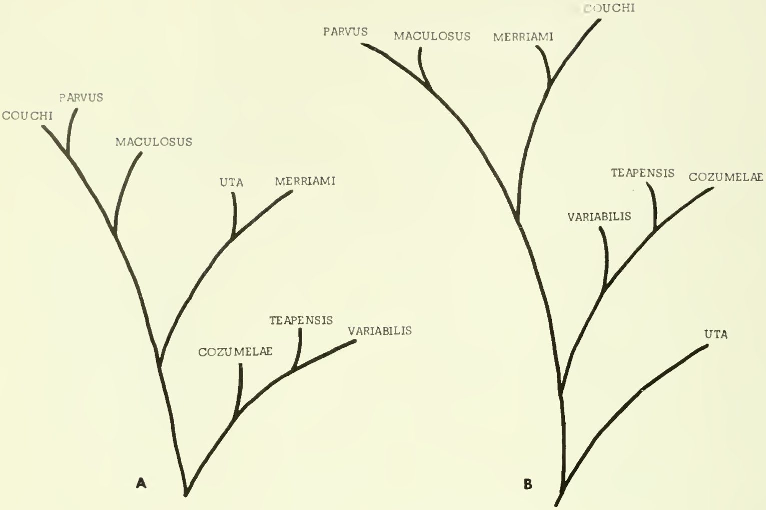
PARVUS
COUCHI
MACULOSUS
UTA
MERRIAMI
TEAPENSIS
VARIABILIS
COZUMELAE
A
COUCHI
PARVUS
MACULOSUS
MERRIAMI
TEAPENSIS
COZUMELAE
VARIABILIS
UTA
B

Fig. 6. Phylogeny of Smith's (1939) *variabilis*, *maculosus*, and *merriami* groups according to Smith (A) and the new phylogeny (B).

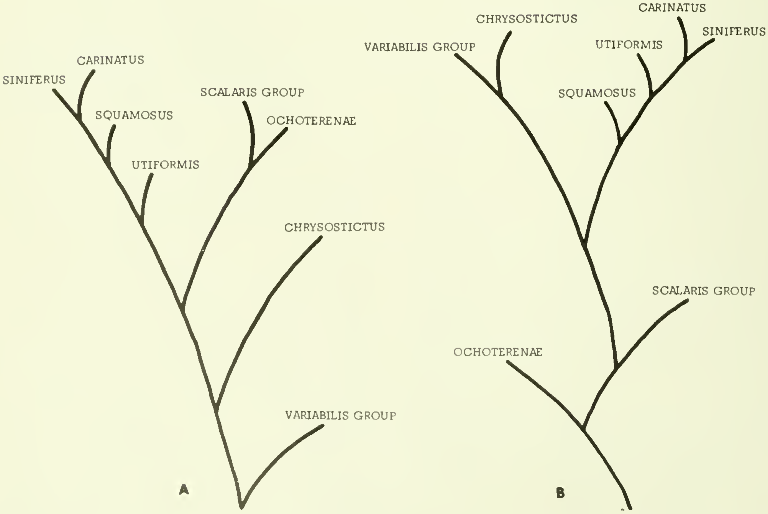
CARINATUS
SINIFERUS
SQUAMOSUS
UTIFORMIS
SCALARIS GROUP
OCHOTERENAE
CHRYSOSTICTUS
VARIABILIS GROUP
A
CHRYSOSTICTUS
VARIABILIS GROUP
CARINATUS
SINIFERUS
UTIFORMIS
SQUAMOSUS
SCALARIS GROUP
OCHOTERENAE
B

Fig. 7. Phylogeny of Smith's (1939) *chrysostictus*, *utiformis*, and *siniferus* groups according to Smith (A) and the new phylogeny (B).

Group I includes: *parvus, couchi, maculosus, merriami, ochoterenae, jalapae,* and *gadoviae*, the most primitive. Smith (p. 362) included *gadoviae* with *nelsoni* and *pyrocephalus* in the *pyrocephalus* group. But once again he outlined reasons why *gadoviae* could be removed and placed in Group I. "*S. gadoviae* differs widely from other members of the group in having very small dorsal scales, a large number of femoral pores, a postfemoral dermal pocket, very small scales on posterior surface of the thighs, and many other minor characters." *S. gadoviae* is also the only member of this group to have a vestigial gular fold as mentioned by Smith (p. 374): "scales immediately preceding gular fold region somewhat reduced in size." All of these characters are diagnostic of Group I, and this primitive placement is therefore natural. In fact, Smith (p. 363) said, "I assume *gadoviae* to be nearest the primitive type, as it retains certain characters of the *variabilis* group, from which I believe it was derived."

The main character on which Smith (p. 363) based his inclusion of *gadoviae* with the *pyrocephalus* group is the strong compression of the tail: "That the group is a natural one is more or less assured by its compact range and by the common character of the compressed tail, which is otherwise unknown in the genus." In view of the many characters supporting the placement of *gadoviae* in Group I, we propose that a compressed tail developed twice: once in the *pyrocephalus* group, and once in *gadoviae*. Smith (p. 363) gave further support to this placement of *gadoviae*: "The assumption that *gadoviae* is a remnant of a primitive stock is supported by its secretive habits and its restriction to a somewhat arid region."

The most serious difference between the new phylogeny and that of Smith is the placement of the *grammicus* and *megalepidurus* groups. In both phylogenies the species are arranged in a similar manner within these groups. But Smith placed these groups next to the *formosus* group with the large-scaled, large-sized species, and we have moved them to a primitive position in Group II. However, we propose that the *grammicus* group (we have combined Smith's *grammicus* and *heterolepis* groups) is the most primitive in Group II. In fact, Smith (1938:552) said "the *microlepidurus* [our *grammicus*] group is assumed to be the most primitive of these [the large-scaled, large-sized species], largely because of its very small scales." This greater separation between the *grammicus* and *formosus* groups is further justified by the fact that the diploid number of chromosomes is 22 (derived) in the *formosus* group and 32 (primitive) in the *grammicus* group. We propose, therefore, that some of the similarities between *grammicus* and *formosus* (coloration, dorsal-scale count, ovoviviparity, and preference for an arboreal habitat) are a result of convergence as is true of *gadoviae* and the *pyrocephalus* group.

The only remaining difference from Smith's *formosus* group is his inclusion of *asper*, which we have moved to the *grammicus* group. This move is justified by the fact that *asper* has 32 chromosomes, as do the other members of the *grammicus* group. If the *grammicus* group is removed from Smith's large-scaled, large-sized branch, the remaining species are the same as those included in Group III. This grouping (the omission of *grammicus*) was allowed by Smith (1938:552):

> The relatively small size of the species of the *undulatus* group must be assumed as a parallel development rather than a direct inheritence of the small size of the ancestor in the *variabilis* group, for the close relationship of the *spinosus* and *undulatus* groups cannot logically be disputed, nor is the close relationship of the *spinosus*, *torquatus* and *formosus* groups doubtful."

Smith and Taylor (1950) included the following species within the *undulatus* group: *undulatus, cautus, occidentalis,* and *woodi*. Since then, *virgatus* has been raised from subspecific to specific status (Cole, 1963). Smith (1939) placed *graciosus* adjacent to the *undulatus* group, so the only discrepancy between the two classifications is the placement of *cautus*, which we have moved to the *spinosus* group next to *olivaceus*. This movement is justified by the fact that there is a zone of intergradation between *cautus* and *olivaceus* (Hall, pers. comm.).

Bussjaeger (1971:151) remarked:

> The relation of *cautus* and *olivaceus* and the *undulatus* group of *Sceloporus* has been questioned. Hall's data indicated that these two species were the same and limited data on their displays indicate that they are similar. If one accepts that they are syn-

> onyms, then *olivaceus* (*cautus*) would be the connecting link between the *spinosus* and *undulatus* groups.

However, rather than use these forms as a link between species groups, we have placed them together in the *spinosus* group.

Smith (1938:554) indicated that the *torquatus* group consited of 2 subgroups: "It appears that soon after the separation of the *torquatus* stock from the other groups of *Sceloporus*, there was a separation into two divisions, one of which exhibited a tendency to develop small scales, the other large scales." We have recognized the small-scaled division as the *jarrovii* group.

Figure 8 shows the phylogeny of the *jarrovii* group according to Smith (1938, Fig. 4) and the new arrangement. Although he placed *lineolateralis* further away from *jarrovii* in his diagram, Smith (p. 556) did say, "*S. jarrovii* appears to be most closely related to *lineolateralis*. From this species, or its ancestors, the remaining species of the small-scaled division have obviously been derived."

Figure 9 shows the phylogeny of the *torquatus* group according to Smith (1938, Figs. 3-4) and the new arrangement. There seems to be little similarity here, except that *torquatus* is derived from *serrifer*, and *poinsetti* is derived from *cyanogenys* in both trees. Smith (1938: 555) raised a question about the ancestral position of *serrifer*:

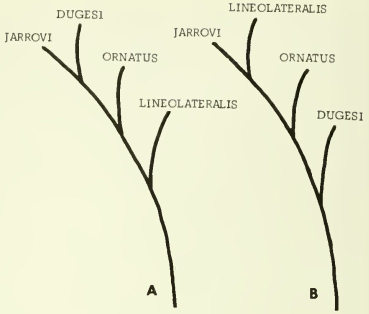
DUGESI
JARROVI
ORNATUS
LINEOLATERALIS
A
LINEOLATERALIS
JARROVI
ORNATUS
DUGESI
B

Fig. 8. Phylogeny of *jarrovi* group according to Smith (1938) (A) and the new phylogeny (B).

> *S. serrifer* appears to be the oldest of the large-scaled species. The postulation that this species, which is one of the larger ones

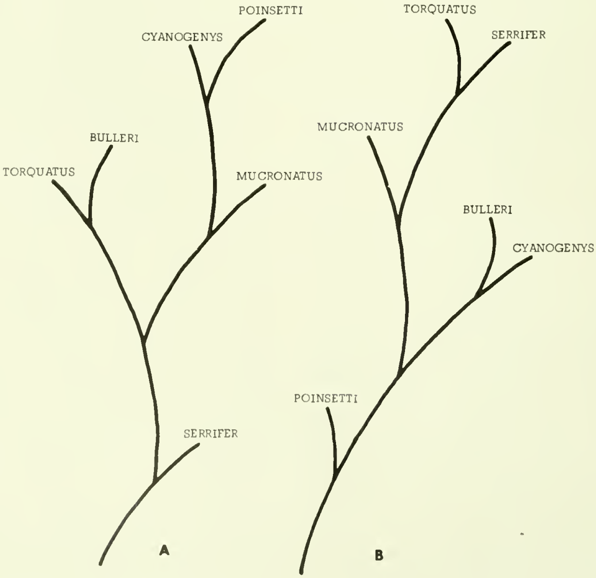
POINSETTI
CYANOGENYS
BULLERI
TORQUATUS
MUCRONATUS
SERRIFER
A
TORQUATUS
SERRIFER
MUCRONATUS
BULLERI
CYANOGENYS
POINSETTI
B

Fig. 9 Phylogeny of *torquatus* group according to Smith (1938) (A) and the new phylogeny (B).

> of the genus, and one having large scales, is nearest to the ancestral type of the large-scaled division of the *torquatus* group may appear to be contradictory to the postulation that *Sceloporus* is derived from small species with small scales. However, my assumption seems to be justified by the fact that *serrifer* occupies a southern position on the periphery of the geographical area now occupied by the *torquatus* group.

The reason for this paradox is that Smith assumed speciation in Group III was from south to north. The data in 1938 strongly supported this conclusion. Obviously, Smith did not believe that a peripheral location is necessarily primitive, because on the next page (556) he said, "*S. mucronatus* appears to be the nearest to the ancestral type of these three species (*cyanogenys*, *poinsetti* and *omiltemanus*) despite the fact that it has larger scales than they. I so conclude because of its centralized geographical position with relation to the area occupied by the other three forms."

So the basic problems can be solved, and the trend is indeed from small to large size and small to large scales if this group was developed from north to south rather than south to north. Smith indicated a northward development from *serrifer* to *torquatus* to *mucronatus* to *cyanogenys*, and our phylogeny indicates a southward development from *cyanogenys* to *mucronatus* to *serrifer* to *torquatus*. An ancestral placement of *cyanogenys* is further supported by Smith (1939:209): "Species of this group are as a rule confined to rocky habitats. So far as I am aware, only *cyanogenys* tends to live on or near the ground." Thus, the new phylogeny indicates a trend in this group from small-sized, small-scaled ground dwellers to large-sized, large-scaled rock dwellers. With this reversal in direction, the remaining differences between the two phylogenies in Figure 9 are negligible and the trends within this group fit the overall phylogeny of the genus.

In the genus *Sceloporus*, the *spinosus* group has been the object of more systematic study than any other. No less than four different phylogenetic trees have been proposed by Smith, Bussjaeger, Cole, and Hall. The confusion is further compounded by the fact that the *spinosus* group is the largest in number of species and subspecies. The four phylogenetic trees and our conclusions are presented in Figure 10. Smith (1939) included *acanthinus*, *lunaei*, and *lundelli* with this group. In 1950, he and Taylor moved *acanthinus*

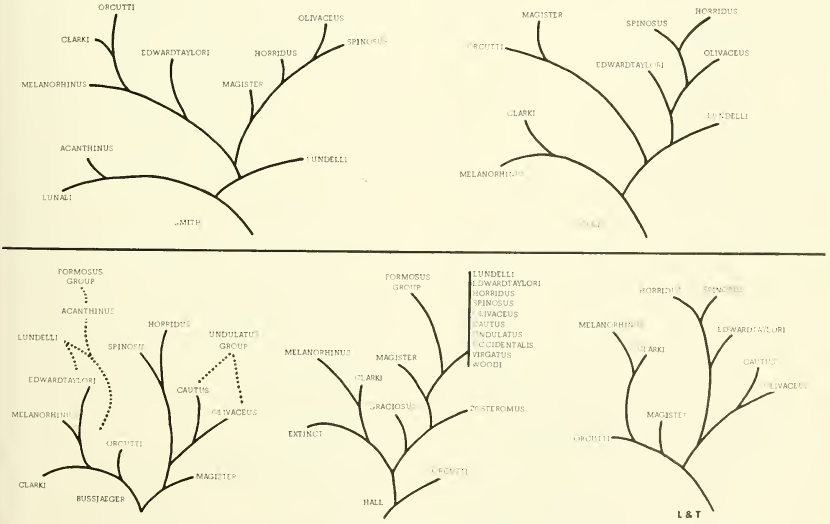
ORCUTTI
CLARKI
EDWARDTAYLORI
HORRIDUS
OLIVACEUS
SPINOSUS
MELANORHINUS
MAGISTER
ACANTHINUS
LUNDELLI
LUNAEI
SMITH
MAGISTER
ORCUTTI
SPINOSUS
HORRIDUS
EDWARDTAYLORI
OLIVACEUS
CLARKI
LUNDELLI
MELANORHINUS
FORMOSUS GROUP
ACANTHINUS
LUNDELLI
HORRIDUS
SPINOSUS
UNDULATUS GROUP
EDWARDTAYLORI
CAUTUS
MELANORHINUS
OLIVACEUS
ORCUTTI
MAGISTER
CLARKI
BUSSJAEGER
FORMOSUS GROUP
LUNDELLI
EDWARDTAYLORI
HORRIDUS
SPINOSUS
OLIVACEUS
CAUTUS
UNDULATUS
OCCIDENTALIS
VIRGATUS
WOODI
MELANORHINUS
MAGISTER
CLARKI
GRACIOSUS
ZOSTEROMUS
EXTINCT
ORCUTTI
HALL
HORRIDUS
SPINOSUS
MELANORHINUS
EDWARDTAYLORI
CLARKI
CAUTUS
OLIVACEUS
MAGISTER
ORCUTTI
L & T

Fig. 10. Phylogeny of *spinosus* group according to Smith (1939), Cole (1970), Bussjaeger (1971), Hall (pers. comm. 1973), and the new phylogeny (L and T).

and *lunaei* into the *formosus* group. However, in 1939 Smith (p. 60) said, "The most primitive form of the group is undoubtedly *lunaei*, which is closely related to *formosus malachiticus*. *S. acanthinus* is a near relative of *lunaei*, as is also *lundelli*." It should therefore be acceptable to remove *lundelli* from the *spinosus* group and place it in the *formosus* group next to *lunaei* as we have done.

Behavioral data also support this arrangement. Bussjaeger (1971:136) observed:

> The display-action-patterns of *lundelli gaigei* of the *spinosus* group and *asper*, *acanthinus acanthinus* and *a. lunaei* of the *formosus* group were quite similar with peaked single units and multiple units. *Sceloporus asper* and *lundelli* seemed to share more elements.

In his conclusions, Bussjaeger (p. 151) anticipated the new position of *S. lundelli*:

> The status of *lundelli* is questionable. . . . Its display-action-pattern was between *acanthinus* and *orcutti;* but the pattern was based on only one female. More data are needed to establish this species relationship. At present it should be left in the *spinosus* group, although it appears to be closer to the *formosus* group.

Cole's (1970) phylogenetic tree would not allow the removal of *lundelli* from this group unless *melanorhinus* and *clarki* were placed elsewhere. Cole (p. 39, Fig. 17) showed how four centric fusions could change the *melanorhinus-clarki* karyotype into the typical pattern for this group. According to Cole's assumption that only fusions (i.e., no fissions) are possible, *melanorhinus* and *clarki* are primitive not only for this group, but also for the genus *Sceloporus*, and for the entire family Iguanidae! As demonstrated by Webster, Hall, and Williams (1972), chromosomal evolution can occur by fission as well as fusion. We believe this is the only acceptable explanation for the karyotype in *melanorhinus* and *clarki*. If fission is accepted as well as fusion, Cole's data provide support for our arrangement of *orcutti*, *clarki*, and *melanorhinus*. (They also confirm the primitive position of *lundelli* and permit its placement in the *formosus* group.)

If *clarki* and *melanorhinus* are derived from *orcutti* and if *lundelli* is removed from the group, then the only difference between Cole's tree and ours is a minor shift in the position of *edwardtaylori*. The single remaining difference between Smith's tree and ours is the placement of *edwardtaylori*. The close relationship of *edwardtaylori* to *spinosus* and *horridus* has been proposed by Cole and also by Hall. The justification is that the species clustering on one side (*olivaceus*, *cautus*, *edwardtaylori*, *spinosus*, and *horridus*) all have 22 chromosomes, whereas *orcutti* has 34, *magister* has 26, and *clarki* and *melanorhinus* each have 40.

ZOOGEOGRAPHY

The phylogeny of the genus *Sceloporus* can be considered with its present geographical distribution to produce a theoretical history of events in the speciation in this genus. We conclude that the ancestral sceloporine was a tropical or subtropical lizard (as Smith reasoned) with a distribution somewhat matching the subtropical conditions of western America before the Madro-Tertiary revolution (Ballinger and Tinkle(1972:63). This distribution was not restricted to southern Mexico, where Smith proposed the beginning of *Sceloporus* evolution, but covered a vast area in the western United States extending as far north as Canada.

Milstead (1960:76) said, "Formation of the western deserts is presumed to have begun in Miocene times and continued through Pliocene and into early Pleistocene times." Accordingly, the derivation of the Scelporine genera could have occurred in late Miocene and early Pliocene times during the development of the western deserts (Ballinger and Tinkle, 1972).

The formation of deserts trapped a mesic-adapted relict (*Petrosaurus*) in Baja California. The remaining sceloporine stock began adapting to the oncoming desert conditions with such characters as a lengthened, sinuous nasal passage and the behavior called "shimmy burial" (Stebbins, 1944). The separation of the generic lines of *Uta*, *Urosaurus*, *Sator*, and *Sceloporus* was accomplished during the initial stages of adaptation to desert conditions.

As tropical conditions moved southward during middle and late Pliocene (Axelrod, 1948), the ancestral stock of Group I moved south almost as far as the Isthmus of Tehuantepec. Some populations did not migrate, but remained and adapted to more xeric conditions (Group III). The mountains of central and southern Mexico provided a barrier that separated the western Group I and eastern Group II populations. A relict genus (*Sator*) was isolated in Baja California at this time (Fig. 11). The subsequent development of Groups I and II was a matter of adaptive radiation and centrifugal speciation (Brown, 1957).

Figure 12 shows the routes of speciation in Group I. The eastern branch extended from *gadoviae* (in southern Michoacan, Guerrero, Morelos, southern Puebla, and northwestern Oaxaca) northward across the Oaxaca Upland, the Neovolcanic Plateau and into the Sierra Madre Oriental to *parvus* (in Nuevo Leon, southeastern Coahuila, San Luis Potosi, and Hidalgo). Speciation continued northward along the Sierra Madre Oriental to *couchi* (Nuevo Leon, eastern Coahuila, and southern Texas) and *merriami* (northern Coahuila and adjacent Texas). (Locality information in this discussion is from Smith and Taylor, 1950. Topographical terminology is from Raisz, 1964.)

The second branch of Group I extended from *parvus* to *jalapae* (Veracruz, Puebla, and Oaxaca). This radiation then moved across the Mixtec Upland (along the northern border of Oaxaca) and northward along the western flank of the Sierra Madre del Sur (through Guerrero, Michoacan, Colima, and Jalisco) and further northward along the western flank of the Sierra Madre Occidental (through Nayarit and Sinaloa and into Durango). The Durango populations became *maculosus*, and most of the pathway is now occupied by *ochoterenae*.

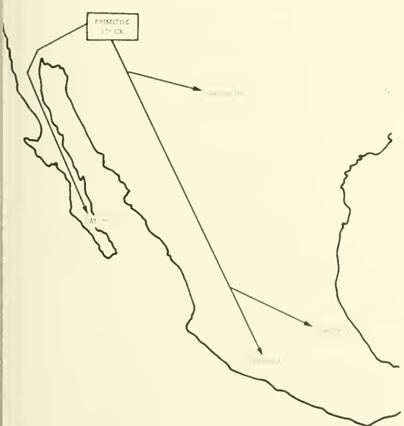

Fig. 11. Isolation of early *Sceloporus* stocks in response to desert formation in middle Pliocene.

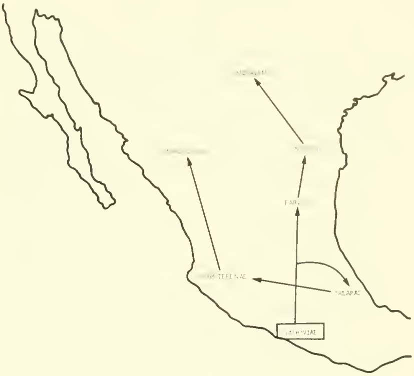

Fig. 12. Speciation in Group I.

Figure 13 shows the initial radiation from the ancestral stock of Group II. This ancestral stock is now represented by *pictus* (in central Puebla and central western Veracruz). The first radiation involved four species in four directions: *aeneus* to the north, *pyrocephalus* to the west, *siniferus* to the south, and *cozumelae* to the east.

Subsequent radiation from these centers is shown in Figure 14. *Sceloporus aeneus* (Puebla, Veracruz, Oaxaca, Hidalgo, Morelos, Mexico, Guanajuato, Michoacan, and Jalisco) produced *scalaris* (in Durango, Guanajuato, Hidalgo, Jalisco, Mexico, Michoacan, Puebla, and Zacatecas). *S. pyrocephalus* (Guerrero, Michoacan, and Colima) produced *nelsoni* (in Chihuahua, Jalisco, Sinaloa, and Nayarit).

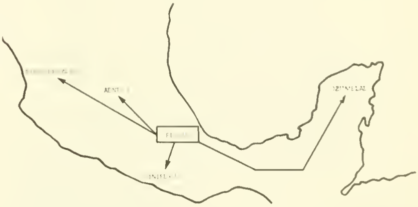

Fig. 13. Early radiation in Group II.

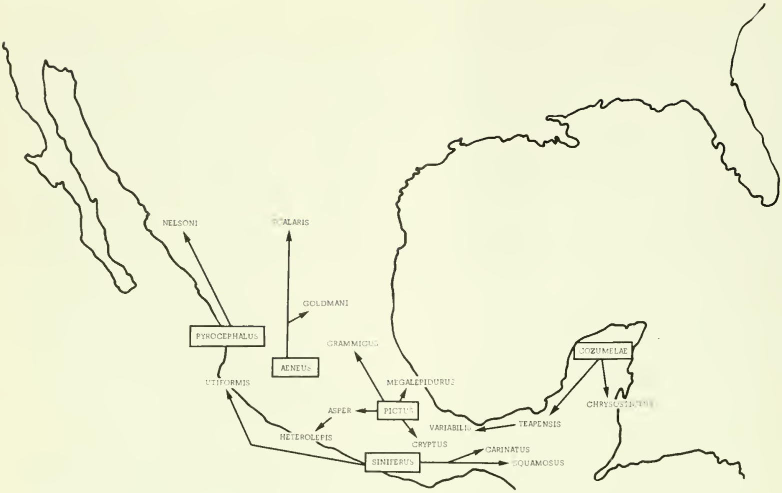

Fig. 14. Second radiation in Group II.

These two species occupy most of the western flank of the Sierra Madre Occidental. According to Hall, the separation of *nelsoni* and *pyrocephalus* occurs along a river in Nayarit (the Rio Grande de Santiago). Concerning this river, Hall (pers. comm., 1973; see also Hall, 1973: 115-125) said:

> Evidence from the fresh water fish fauna in the Rio Grande de Santiago (Salvador Contreras B., pers. comm.) suggests that at one time this major river drained the greater part of the Mexican Plateau. Even now it is the outlet for Lake Chapala and the entire Rio Lerma extending east as far as the western border of the Distrito Federal. Although rivers usually are not very effective natural barriers, the steep gradient of this river as it falls off the Plateau and the comparative narrowness of the costal plain probably would have made it an extremely effective barrier during the Pleistocene pluvial times, which would have provided ample opportunity for the splitting of the proto-*nelsoni* into two stocks.

The southern speciation produced *siniferus* (in Oaxaca, Chiapas, and Guerrero), *carinatus* (in Chiapas), *squamosus* (along the Pacific slopes from Chiapas to Costa Rica), and *utiformis* (to the north along the Pacific slopes of Michoacan, Colima, Jalisco, Nayarit, and Sinaloa). The eastern branch to *cozumelae* (in the northern peninsular states of Yucatan and Quintana Roo) produced *chrysostictus* (in the entire Yucatan Peninsula), *teapensis* (in southern Veracruz, Tabasco, Campeche, Quintana Roo, northern Guatemala, and British Honduras), and *variabilis* (which has developed subspecies along the Gulf Coast plain from south-central Texas, through Nuevo Leon, Tamaulipas, San Luis Potosi, Queretaro, Hidalgo, Tlaxcala, Puebla, and Veracruz, across the Isthmus of Tehuantepec, through Oaxaca and Chiapas, and into western Guatemala).

The central stock of Group II also produced a second wave of speciation. A southern speciation from *pictus* produced *cryptus* in the Oaxaca highlands. A western speciation resulted in *asper* (in the Sierra Madre del Sur in Guerrero and Michoacan and extending as far north as the Sierra Madre Occidental in Nayarit). This branch also produced *heterolepis* in the coastal mountains of Jalisco.

An eastern branch from *pictus* produced *megalepidurus* in Northern Puebla on the eastern slopes of the Neovolcanic Plateau. The most recent derivation from the *pictus* stock is *grammicus*. This species has invaded most of the Plateau regions in Mexico. The distribution of *grammicus* is widespread, and Hall (1971) has suggested that there may be as many as 6 cryptic species in the *grammicus* complex. Further discussion of this species must therefore be deferred until the alpha taxonomy is more complete.

Speciation in Group III was more complex and probably more recent than in the others. Other workers have suggested that considerable speciation resulted from repeated glaciation in Pleistocene times (Savage, 1960; Ballinger and Tinkle, 1972). Each glacial period forced desert species into southern refugia from which they later speciated through adaptive radiation and centrifugal speciation.

Group III remained originally in the north and adapted to the xeric conditions of the southwest during middle and late Pliocene, as did *Uta* and *Urosaurus*. Subsequent Pleistocene glaciation forced the desert-adapted populations into southern refugia with massive northern extinctions. The five refugia south of 30° latitude include Baja California, the Sonoran Desert, the Mexican Plateau, the Gulf Coastal Plain, and Florida. Barriers include the Gulf of California, the Sierra Madre Occidental, the Sierra Madre Oriental, and the Gulf of Mexico. Ballinger and Tinkle (1972) discussed the first three refugia in considerable detail with reference to the evolution of *Uta*.

After each glacial period, the isolated populations expanded in all directions from their refugia. (A worldwide increase in rainfall would restrict the midlatitude deserts from both sides. A subsequent decrease in rainfall would cause a movement of xeric conditions both northward and southward from a small latitudinal band.) Each southerly movement was preserved as the species adapted to subtropical conditions, but the northerly radiations would be eliminated during the next glacial period (southern rains could be tolerated better than northern snows).

Each invasion to the south required a secondary adaptation to the ancestral environment. This explains why *formosus* has not yet lost a behavioral trait called "shimmy burial." Hall (pers. comm.; see also Hall 1973:99-102) said:

> One gathers from Cole's (1970) discussion that he uncritically accepts Smith's (1939) idea that the arboreal, tropical *formosus* group is primitive in the genus. Smith (pers. comm.) believed, not unreasonably on the limited information then available, that the closest primitive relatives of *sceloporus* were the South American tropidurines (from which Weigmann separated *Sceloporus*), and that its close xeric adapted relatives (i.e. "*Uta*" = *Petrosaurus*, *Urosaurus*, and *Uta*) were derived from within the radiation of *Sceloporus*. The work of Savage (1958), Etheridge (1964), and Presch (1969) tends to refute this idea. . . .
>
> Furthermore, it is interesting to note that the behavioral trait of 'shimmy burial' . . . is also found in most other Sceloporines. . . .
>
> From this analysis, it would seem that all sceloporines above *Petrosaurus* at least primitively know how to use loose sand for escape and sleeping cover. It seems unlikely that this behavior would evolve in a supposedly primitive form like *formosus*, which lives in mountain rain forests where the lizards would rarely or never encounter a suitable substrate for shimmy burial. Its presence in this species probably indicates only that *formosus* has only very recently entered the rain forest habitat. On the other hand, shimmy burial would be selectively valuable to a species inhabiting dry plains or deserts where loose sand might frequently be the only cover available for escape or sleeping.

This quotation explains why Smith (1939) and Cole (1970) proposed phylogenies from south to north. We propose a reversal of these phylogenies, which means that most trends in Group III are from the north and that the Group III forms moved southward and adapted to a climate similar to the one in which the ancestors lived.

The smaller size and greater isolation of Baja California have limited the genetic potential of its populations. This has allowed continental species to move north from the Sonoran Desert and enter the peninsula to trap southern relicts (see Savage, 1960).

Another possible explanation for relict species in Baja California is the separation and westward drift of the peninsula in Miocene-Pliocene times. Concerning this movement, Moore and Buffington (p. 1241) said, "Therefore, from about 4 to 10 million years ago, during late Miocene and Pliocene times, a proto-Gulf of California existed. . . . The present cycle of spreading began about 4 million years ago."

Tanner (1966:191) stated that this same event could apply to the night snakes:

> Thus the distribution of *Eridiphus* stock may have reached southern Baja California by a shorter route before the present Gulf of California was formed. Assuming this to be correct, *Eridiphus* is a relic of a once more widespread group of snakes in Western Mexico.

Hall (1973) has suggested that such a mechanism is responsible for speciation in Baja California and that the Cape region was isolated from the rest of the peninsula as well as the mainland during an intermediate stage.

The first glacial advance divided *Sceloporus* into four refugia: an *orcutti* stock in Baja California, a *formosus* stock in the Sonoran Desert, a *virgatus* stock on the Mexican Plateau and a *cyanogenys* stock on the Gulf Coastal Plain. Subsequent postglacial speciation is illustrated in Figure 15.

The *virgatus* stock expanded northward and as far eastward as Florida. It also expanded westward into the Sierra Madre Occidental. Most of the expansion from this stock was reduced to refugia during a second glacial advance. The second glacial advance was less severe than the first (Ballinger and Tinkle, 1972:63) and a population survived in Florida (*woodi*). The main *virgatus* stock was again confined to the Mexican Plateau, but some of the mountain populations moved west into the Sonoran refuge. This isolation produced *graciosus*.

The subsequent northward migration of *graciosus* and the northern speciation of *undulatus* and *occidentalis* from *virgatus* is shown in Figure 16.

The *orcutti* stock, which was confined to the Baja California refuge during the first glaciation, emerged with sufficient adaptive specialization to displace the *formosus* stock as far south as Guerrero. The displacement of a mainland population by a restricted peninsular population is explained by the assumption that *formosus* descended from the part of the *Sceloporus* stem that had been adapting to the mountain habitat between the central plains and the western deserts. As the Pacific slopes became more and more arid following glacial retreat, the desert-adapted *orcutti* stock displaced the mountain-adapted *formosus* stock.

From the Pacific slopes in Guerrero, the *formosus* stock speciated southward, producing *formosus* (with subspecies in Guerrero and the central uplands of Oaxaca), *malachiticus* (along the Pacific slopes from Chiapas to Panama), *lunaei* (in the uplands of central Guatemala), *lundelli* (in the central regions of the Yucatan Peninsula), and *tanneri* in Oaxaca (Smith and Larsen, 1975).

Farther north along the Pacific Coast, the *orcutti* stock produced *clarki* (from central Arizona, through the center of Sonora and down the Pacific Coast of Sinaloa to Nayarit) and *melanorhinus* (along the Pacific slopes from Nayarit

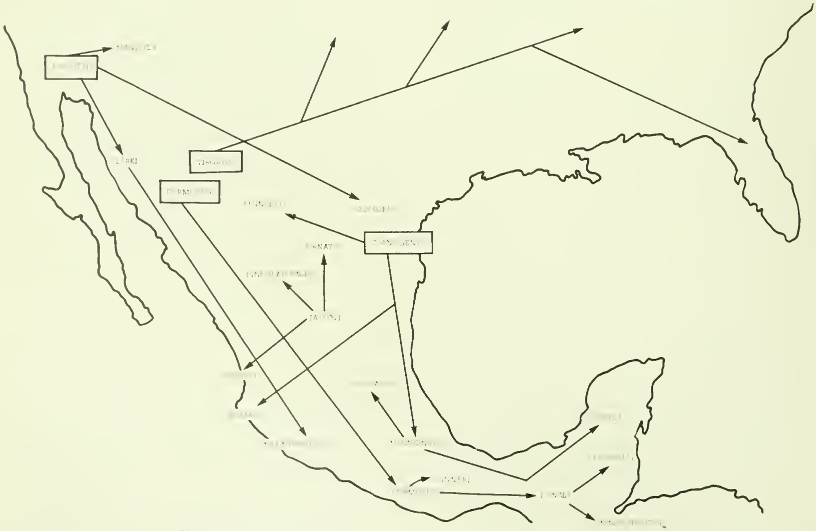

Fig. 15. Early radiation in Group III.

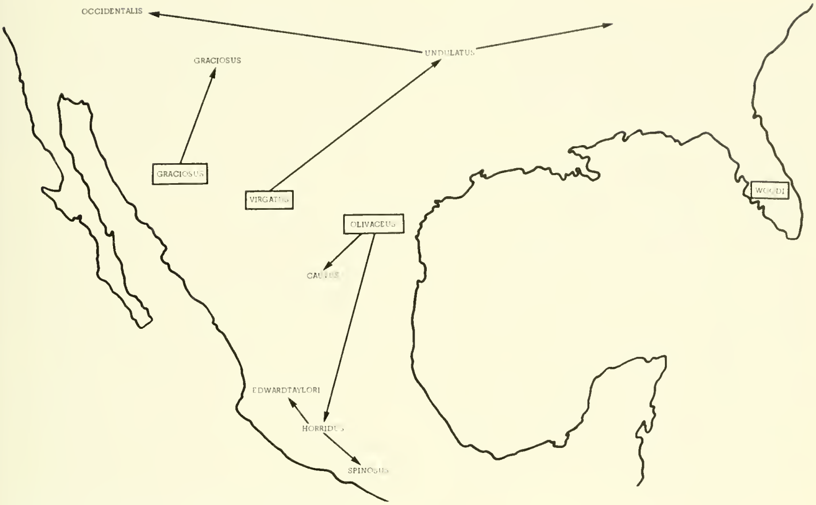

Fig. 16. Second radiation in Group III.

through Jalisco, Colima, Michoacan, Guerrero, and Oaxaca to Chiapas). Hall's comments about the separation of *nelsoni* and *pyrocephalus* along the Rio Grande de Santiago are also appropriate for *clarki* and *melanorhinus*. Apparently this river was a geographic barrier for two groups speciating in opposite directions.

Another branch from the *orcutti* stock produced the *magister* complex. The subsequent subspeciation of *magister* according to Phelan and Brattstrom (1955) was from central California southward into Baja California and southeastward into Arizona and New Mexico. However, *orcutti* has 34 chromosomes, *magister zosteromus* (and all other peninsular subspecies of *magister*) has 30, and *m. magister* has 26. This supports Hall's phylogeny with early speciation in Baja California and subsequent emergence of two stems (*orcutti* and *magister*).

A third and final branch from the *orcutti* stock moved eastward through the interglacial deserts of Arizona, New Mexico, and Texas. This branch (*olivaceus*) became trapped in the Gulf Coastal Plain refuge during the second glacial period (Fig. 15). Speciation proceeded from *olivaceus* (central Texas, Tamaulipas, Nuevo Leon, and adjacent states) southward across the Central Meseta to *spinosus* (occupying the entire Neovolcanic Plateau from Puebla and Veracruz on the east to the tip of Durango on the west), *horridus* (with subspecies along the entire southern flank of the distribution of *spinosus*), and *edwardtaylori* (in Oaxaca) (Fig. 16).

A secondary speciation from *olivaceus* (to *cautus*) has been questioned by Hall (because of intergrades), but he (pers. comm., 1973) did make this observation:

> Most interestingly there seems to be almost no question that *cautus* and *olivaceus* intergrade south and west of Monterrey (Nuevo Leon) with gene flow occurring presently through the dry valleys and passes. There might be an absolute classic circle of subspecies whose terminal populations are fully sympatric.

The last major speciation within *Sceloporus* started with *cyanogenys* in the Gulf Coastal Plain refuge (Fig. 15). The first branch produced *jarrovi* (in the northern plateaus and adjacent escarpments from Arizona on the northwest to Veracruz on the southeast), which in turn produced *ornatus* (in the ranges of southern Coahuila), *lineolateralis* (restricted to the mountains of eastern Durango), and *dugesi* (with subspecies in the mountains of Guanajuato, Michoacan, Colima, Jalisco, and Nayarit.)

The second branch from *cyanogenys* moved westward to produce *poinsetti* (which occupies most of the northern

Plateau through southern New Mexico, southwestern Texas, and the Mexican states of Chihuahua, Coahuila, and Durango). The third branch extended across Mexico in a southwesterly direction and resulted in *bulleri* (in the mountains of Jalisco).

The final radiation from the *cyanogenys* stock extended southward and resulted in *serrifer* (occupying most of the Gulf Coastal Plain in Tamaulipas, San Luis Potosi, Veracruz, Tabasco, Campeche, and Yucatan), *mucronatus* (a mountain form in the Oaxaca Upland and other mountains in the state of Guerrero, Veracruz, Puebla, Mexico, and Hidalgo), and *torquatus* (which inhabits a large area in central Mexico, including parts of Hidalgo, Veracruz, Mexico, Distrio Federal, Puebla, Morelos, Guanajuato, Michoacan, Nuevo Leon, Jalisco, San Luis Potosi, and Zacatecas).

CONCLUSIONS

When presenting his arrangement, Smith (1939) said, "Material from certain areas is still lacking, and more direct evidence of relationships is frequently to be desired. The conclusions now presented are accordingly tentative." Smith's statement may still apply. Problem areas include Baja California and the *grammicus* complex. Also several new species and subspecies are being considered by various workers. New kinds of data are now being researched (microdermatoglyphics, for example). However, a point has been reached at which different sets of data reinforce similar conclusions. With over 80 characters, the new groups and subgroups are distinct at the .999 level of confidence (Larsen and Tanner, 1974). With such a high level of confidence, we conclude that Figure 5 is a natural arrangement of species and that future adjustments may be minor.

When phylogeny and zoogeography are considered simultaneously, several trends are evident in the evolution of *Sceloporus*: (1) the size altered from small to large; (2) the scales, once small, smooth, and granular, changed, becoming large, carinate, mucronate, and imbricate; (3) initial movement and speciation was from north to south, and several secondary radiations were from southern centers northward and from northern centers southward; (4) the geography of Baja California created several relicts; (5) habitat preference changed from ground to rocks, cliffs, and trees; and (6) the ancestral stock, which originally was subtropical, adapted to arid conditions, and then several groups returned to tropical or subtropical climates.

Cope (1900) called *Sceloporus* the *piece de résistance* for the theory of derivation of species. This genus seem to show such principles as parallelism, convergence, divergence, genetic drift, geographical barriers, adaptive radiation, centrifugal speciation, and waif and relict population development. In fact, the cape region of Baja California may provide examples of speciation by continental drift. *Sceloporus* also exhibits a high degree of chromosomal variation, including examples of Robertsonian fission and fusion, and several formulae for sex determination. This genus is extremely well suited for illustration and discussion of evolutionary theory.

We conclude that *Sceloporus* has recently speciated in an explosive manner. Because of this rapid adaptive radiation, it is difficult to determine phylogenetic relationships with classical techniques.

We are persuaded, however, that the genus *Sceloporus* does contain three distinct monophyletic groups. Group I is distinct from the other two groups in having (1) a postfemoral dermal pocket and less than 7 ventrals between the femoral pore series or (2) (if the postfemoral dermal pocket is absent) a vestigial gular fold and no postrostrals. The rest of the species in the genus *Sceloporus* lack either a postfemoral dermal pocket or a vestigial gular fold. If they lack the vestigial gular fold, postrostrals are present and there are more than 8 ventrals between the femoral pore series. In considering the systematics of the entire complex, we believe that it is now feasible to recognize for Group I (Table 1) the Cope (1888) monotypic generic designation of *Lysoptychus* (*L. lateralis*=*Sceloporus couchi* Baird, 1858).

We have not by our methods been able to arrive at a satisfactory taxonomic division of Groups II and III, even though these groups become separable and distinct by use of multivariate analysis. We believe that Groups II and III represent a large assemblage of species that have evolved more recently but that although the characters between the groups are showing indications of evolutionary separation, they have not reached a point of distinction that permits the development of a workable taxonomic key. We therefore choose at this time to retain them in the genus *Sceloporus*.

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NEW SYNONYMY AND NEW SPECIES OF AMERICAN BARK BEETLES (COLEOPTERA: SCOLYTIDAE)[1]

Stephen L. Wood[2]

ABSTRACT.— New synonymy is proposed as follows: *Pityokteines* Fuchs (=*Orthotomides* Wood), *Araptus foveifrons* (Schedl) (=*interjectus* Wood), n. comb., *Cryptocarenus seriatus* Eggers (=*bolivianus* Eggers), *Hylastes gracilis* LeConte (=*asper* Swaine), *Procryphalus utahensis* Hopkins (=*aceris* Hopkins), *Scolytodes maurus* (Blandford) (=*Hexacolus ellipticus* Eggers), *Scolytus hermosus* Wood (=*sylvaticus* Bright), *Xyleborus adelographus* Eichhoff (=*vitiosus* Schedl), *Xyleborus catulus* Blandford (=*intricatus* Schedl), *Xyleborus nepos* Eggers (=*signatus* Schedl), *Xyleborus titubanter* Schedl (=*dissidens* Wood). The following species and subspecies are named as new to science: *Cnesinus electus* (Costa Rica), *C. pilatus* (Mexico), *Hylastes asperatus* (New Mexico), *Scolytus torulus* (Costa Rica), *S. laetus* (Mexico), *Scolytodes amabilis* and *S. lepidus* (Mexico), *S. obesus* (Panama), *Pseudothysanoes concentralis* and *P. tumidulus* (Mexico), *Thysanoes tuberculatus* (Mexico), *Pityokteines mystacinus* (Washington), *Ips pilifrons* subsp. *thatcheri* (Nevada), *Araptus attenuatus* (Mexico), *A. fossifrons* (Mexico, Guatemala), *Amphicranus parilis* (Mexico), *Corthylus cecropii* (Costa Rica).

On the following pages several newly discovered cases of synonymy and 17 species and 1 subspecies new to science are presented for American Scolytidae. The specific synonymy is presented in alphabetical order for convenient reference. The species new to science represent the genera *Cnesinus* (2), *Hylastes* (1), *Scolytus* (2), *Scolytodes* (3), *Pseudothysanoes* (3), *Thysanoes* (1), *Pityokteines* (1), *Araptus* (2), *Amphicranus* (1), and *Corthylus* (1). The new subspecies is of *Ips pilifrons*. The new species are from the following countries: United States (2), Mexico (10), Costa Rica (3), Panama (1), Mexico and Guatemala (1). The new subspecies is from the United States (Nevada).

NEW SYNONYMY

Pityokteines Fuchs

Pityokteines Fuchs, 1911, Morphologische Studien über Borkenkäfer: I. Die Gattungen *Ips* DeGeer und *Pityogenes* Bedel, p. 33 (Type-species: *Ips curvidens* Germar, subsequent designation by Hopkins, 1914, Proc. U.S. Nat. Mus. 48:127)

Orthotomides Wood, 1951, J. Ent. Soc. Kansas 24:32 (Type-species: *Orthotomicus lasiocarpi* Swaine, original designation). *New synonymy*

The discovery of *mystacinus* Wood, described below, closes the gap in characters between *Pityokteines* and *Orthotomides* to such an extent that the latter name must be placed in synonymy even though *lasiocarpi* (Swaine) entirely lacks the long female frontal hair characteristic of *Pityokteines*. Female *mystacinus* have part of the frontal vestiture elongate and also have two sutures visible on the posterior face of the antennal club.

This generic synonymy necessitates the transfer of *lasiocarpi* from *Orthotomides* to *Pityokteines*.

Araptus foveifrons (Schedl), n. comb.

Thamnophthorus foveifrons Schedl, 1963, Ent. Arb. Mus. Frey 14:161 (Holotype, male; Guadalajara, Jalisco, Mexico; Schedl Coll.)

Araptus interjectus Wood, 1974, Brigham Young Univ. Sci. Bull., Biol. Ser. 19(1):44 (Holotype, male; Volcan de Agua, Guatemala; Wood Coll.). *New synonymy*

When the North and Central American *Araptus* were reviewed for the monograph, two closely related species were found, both of which fit the description of *Thamnophthorus foveifrons* Schedl. It was assumed that the common, widely distributed species of these two was *foveifrons;* the rare one was named *interjectus* Wood. Recently, I had the opportunity to examine the male holotype of *foveifrons* and to compare it to the male holotype of *interjectus*. They represent the same species. The common species with which it had been confused is named below as *Araptus fossifrons*.

Cryptocarenus seriatus Eggers

Cryptocarenus seriatus Eggers, 1933, Orig. Mem. Trav. Lab. Ent. Paris 1(1):10 (Holotype, female; Nouveau Chantier, French Guayana; Paris Mus.)

Cryptocarenus bolivianus Eggers, 1943, Mitt. Münchner Ent. Ges. 33:356 (Holotype, fe-

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[1] Part of this research was sponsored by the National Science Foundation.

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male; Cochabamba, Bolivia; U.S. Nat. Mus.). *New synonymy*

The holotypes of *Cryptocarenus seriatus* Eggers and *bolivianus* Eggers were compared directly to my material from Brazil, Venezuela, and other areas. All represent the same biological species.

Hylastes gracilis LeConte

Hylastes gracilis LeConte, 1868, Trans. Amer. Ent. Soc. 2:174 (Lectotype, female; Tahoe Valley, California; Mus. Comp. Zool., designated by Wood, 1971, Great Basin Nat. 31:145)

Hylastes asper Swaine, 1917, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(1):19 (Holotype, female; Larimer Co., Colorado; Canadian Nat. Coll.). *New synonymy*

The holotype of *Hylastes asper* Swaine is rather different from what the description might lead one to believe. It is virtually identical to the type of *longus* LeConte and well within the range of variability of *gracilis* LeConte. All three types were compared to my material and, in my opinion, represent the same species. The species I have previously treated as *asper* is described below.

Procryphalus utahensis Hopkins

Procryphalus utahensis Hopkins, 1915, U.S. Dept. Agric. Rept. 99:33 (Holotype, female; Alta, Utah; U.S. Nat. Mus.)

Procryphalus aceris Hopkins, 1915, U.S. Dept. Agric. Rept. 99:33 (Holotype, female; Albany, Oregon; U.S. Nat. Mus.). *New synonymy*

Procrophalus aceris Hopkins was named from a series of about six specimens taken from a limb that had been cut in the vicinity of Albany, Oregon. The limb was given to Hopkins who identified it as *Acer macrophyllum* (personal communication from W. J. Chamberlin). Because the strial punctures were slightly larger than usual, I did not associate these specimens with *utahensis* Hopkins until an identical series was taken from *Salix scouleriana* at Dixie Pass, Oregon. This series was compared directly to the type series of *utahensis* and *aceris* and to other series from British Columbia, Quebec, California, Colorado, South Dakota, and Utah. Only one species is represented by this material; all specimens are from *Salix*. Chamberlin, myself, and many others have searched both standing and cut *Acer macrophyllum* on numerous occasions without finding indications of bark beetle activity. The host identification by Hopkins must have been erroneous.

Scolytodes maurus (Blandford)

Prionosceles maurus Blandford, 1897. Biol. Centr. Amer., Coleopt. 4(6):178 (Syntypes; Cerro Zunil and Pantaleon, Guatemala; British Mus. Nat. Hist.)

Hexacolus ellipticus Eggers, 1934, Ent. Blätt. 30:80 (Holotype, male; Turrialba, Costa Rica; Institut für Pflanzenschutzforschung Kleinmachnow). *New synonymy*

The syntypic series of *maurus* (Blandford) and the male holotype of *ellipticus* Eggers were compared to my material taken from southern Mexico to Panama. Only one common species is represented by this material. In all, 158 specimens were examined.

Scolytus hermosus Wood

Scolytus hermosus Wood, 1968, Great Basin Nat. 28:12 (Holotype, male; 2 km N Tlaxcala state line 18 km N Tlaxco, Puebla, Mexico; Wood Coll.)

Scolytus sylvaticus Bright, 1972, Canadian Ent. 104:1489 (Holotype, male; Cerro Potosi, Nuevo Leon, Mexico; Canadian Nat. Coll.). *New synonymy*

The holotype and allotype of *sylvaticus* Bright and three other specimens from the type locality of that species were compared directly to the type series of *hermosus* Wood. While the holotype has abdominal sternum 2 less strongly concave than normal, the other Cerro Potosi specimens and Bright's illustration of a male from the type series (Fig. 1, p. 1490) are normal specimens of *hermosus*. For this reason, *sylvaticus* must be placed in synonymy.

Xyleborus adelographus Eichhoff

Xyleborus adelographus Eichhoff, 1868, Berliner Ent. Zeitschr. 11:400 (Syntypes, female; Brazil; Brussels Mus.)

Xyleborus vitiosus Schedl, 1940, An. Esc. Nac. Cienc. Biol., Mexico 1:367 (Holotype, female; Mexico?; Schedl Coll.). *New synonymy*

The syntype of *adelographus* Eichhoff in the Brussels Museum is 2.8 mm in length; the holotype of *vitiosus* Schedl is 3.5 mm (not 3.7 mm as given by Schedl). Seven specimens in my collection from Colombia are 3.3-3.4 mm, and one from southern Brazil is 3.5 mm. The specimens from Colombia are very slightly stouter, the declivity along the suture is flat, and the punctures on the declivital striae are slightly more deeply impressed. The holotype of *vitiosus* and my Brazilian specimen of *adelographus* are identical in every respect except for size. These specimens are almost identical to the syntype of *adelographus* and are regarded as conspecific. Because extensive collecting has not produced any specimens of this species from Mexico or Central America, because the Mexican origin of the holotype of *vitiosus* is questioned on its locality label, and because the holotype of *vitiosus* resembles specimens from southern Brazil much more closely than it does representatives of this species from Colombia, this species should be dropped from the faunal list of Mexico until more definite evidence of its occurrence in Mexico is found.

Xyleborus catulus Blandford

Xyleborus catulus Blandford, 1898, Biol. Centr. Amer., Coleopt 4(6):216 (Holotype, female; Volcan de Chiriqui, Panama; British Mus. Nat. Hist.)

Xyleborus intricatus Schedl, 1949, Rev. Brasil. Biol. 9:274 (Holotype, female; St. Catarina, Brazil; Schedl Coll.). *New synonymy*

Several specimens in the California Academy of Sciences were identified by Schedl as *Xyleborus intricatus* Schedl. Since these specimens are of *catulus* Blandford, a loan of the holotype of *intricatus* was requested. The specimen received was labeled as a "paratype" of *intricatus* from Nova Teutonia, Santa Catarina, Brazil; however, this species was based on a unique female, and paratypes were not designated in the original description. Because this specimen is also of *catulus*, *intricatus* is tentatively placed in synonymy until the holotype is located.

Xyleborus nepos Eggers

Xyleborus nepos Eggers, 1923, Zool. Meded. 7:198 Lectotype, female; Java; U.S. Nat. Mus., designated by Anderson and Anderson, 1971, Smithsonian Contrib. Zool. 94:21)

Xyleborus signatus Schedl, 1949, Rev. Brasil Biol. 9:278 (Holotype, female; Mexico; Schedl Coll.). *New synonymy*

The holotype of *signatus* Schedl was named from a unique female labeled "Mexico." This specimen is identical to a long series of *nepos* Eggers from Indonesia and the Philippine Islands, some of which were compared directly to the lectotype of *nepos*. Because extensive collecting in Mexico has not produced another specimen of this species, the holotype of *signatus* is considered a mislabeled specimen and should be dropped from the Mexican faunal list until more definite evidence of its occurrence there is found.

Xyleborus titubanter Schedl

Xyleborus titubanter Schedl, 1948, Rev. de Ent. 19:578 (Holotype, female; Mexico; Schedl Coll.)

Xyleborus dissidens Wood, 1972, Brigham Young Univ. Sci. Bull., Biol. Ser. 19(1):41 (Holotype, female; 9 km NE Teziutlan, Puebla, Mexico; Wood Coll.). *New synonymy*

The holotypes of *titubanter* Schedl and *dissidens* Wood were compared directly to one another and were found to represent the same species.

TAXA NEW TO SCIENCE

Cnesinus electus, n. sp.

This species is distinguished from the female holotype of *bisulcatus* Schedl by the more narrowly spaced eyes (above), by the smaller, more abruptly elevated epistomal process (difference very slight), by the very slightly larger, deeper pronotal punctures, by the larger, more widely spaced strial punctures, and by the coarser declivital setae with a complete row of setae on interstriae 1.

FEMALE.— Length 2.5 mm, (paratypes 2.3-2.6 mm), 2.8 times as long as wide; color dark brown, elytra dark reddish brown.

Frons strongly, transversely impressed at level of antennal bases, convex above, somewhat flattened below this point, with epistomal process poorly developed and devoid of granules or tubercles; eyes approximate above, separated by a distance equal to 0.5 times greatest width of an eye (about twice this wide in *bisulcatus*); surface rugulose and rather coarsely punctured above eyes, rugose-reticulate below upper level of eyes, with a few fine punctures along lateral margins and on epistoma; vestiture limited to lateral and epistomal areas. Eyes very large; very coarsely faceted.

Pronotum 1.1 times as long as wide; widest just in front of middle, almost straight from widest point to sharply defined basal angles, somewhat constricted just behind narrowly rounded anterior margin; surface dull, subshining, more distinctly shining toward base, punctures almost round at base, becoming increasingly elongate anteriorly, occasionally confluent in anterior area; glabrous.

Elytra 1.7 times as long as wide; sides almost straight and parallel on basal two-thirds, rather narrowly rounded behind; striae 1 rather strongly, others moderately, not abruptly impressed, punctures small, except on 1 not confluent, distinctly, rather strongly impressed, separated by distances slightly less than their own diameters; interstriae feebly convex, shining, punctures varying from minute to two-thirds size of those of striae, in indefinite uniseriate rows. Declivity convex, except moderately impressed between interstriae 3; striae feebly impressed, punctures rather small but impressed; interstriae 1 abruptly elevated to apex, about half as high as wide, others almost flat, 2 about one and one-half times as wide as 1, twice as wide as 3; all interstriae armed by uniseriate rows of moderately large rounded setiferous granules, each granule about as high as wide, distinctly larger than in *elegans*. Vestiture confined to declivity, except on interstriae 1, consisting of rows of rather coarse, moderately long, interstrial bristles, and short, fine, strial hair.

Female.— Similar to male except epistomal callus more prominent.

Type Locality.— Five miles or 8 km SE Cartago, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and 7 paratypes were taken on 2-VIII-63, at 1500 m, No. 98, from twigs of *Miconia* (?), by S. L. Wood. Seven paratypes bear the same data except that they were from twigs of an unknown tree; five paratypes came from same locality on 29-VII-63, from a woody vine; and seven paratypes are from Peralta, Cartago, Costa Rica, 10-III-64, 500 m, tree seedling, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Cnesinus pilatus, n. sp.

This species is distinguished from *strigicollis* LeConte by the larger size, by the stouter body form, by the different female frons, by the absence of tubercles on declivital interstriae 2, and by other characters noted below.

Female.— Length 3.1 mm, 2.1 times as long as wide; color dark brown, elytra dark reddish brown.

Frons as in *strigicollis* except area below carina slightly less strongly impressed, distance between eyes 0.8 times as wide as width at level of antennal insertion (as in *strigicollis*), carina 0.5 times as wide as distance between eyes, median impunctate area above carina larger, extending above upper level of eyes, vestiture in lateral areas not extending above upper level of eyes and not on median third at vertex (extending well above eyes and almost to median line in *strigicollis*).

Pronotum 0.9 times as long as wide; about as in *strigicollis* except more closely, slightly more coarsely strigose.

Elytra 1.3 times as long as wide, 1.7 times as long as pronotum; similar to *strigicollis* except interstriae three times as wide as striae, declivity more broadly impressed, declivital interstriae 2 devoid of granules, vestiture about half as long, stouter. Interstriae 2 on declivity with a row of punctures, each puncture about two-thirds as large as those of adjacent striae.

Type Locality.— Thirteen km or eight miles W El Palmito, Sinaloa, Mexico.

Type Material.— The female holotype was taken at the type locality on 7-VIII-64, by H. F. Howden.

The holotype is in the Canadian National Collection.

Hylastes asperatus, n. sp.

This is a difficult species to recognize. The very large pronotal punctures are irregular in size, as in *porculus* Erichson, but much closer; the discal interstriae are slightly wider than in allied species, more nearly convex, and very finely, closely crenulate (usually not clearly apparent unless the light source is posterior to the specimen). This species has been treated as *asper* Swaine, but the type of *asper* is quite different.

Female.— Length 4.2 mm (paratypes 4.0-4.6 mm), 2.7 times as long as wide; color dark brown.

Frons as in *gracilis* LeConte with interocular impression moderately strong, fine, low carina evidently always extending from this impression to base of epistomal lobe where it forks as in related species.

Pronotum 1.2 times as long as wide; sides on slightly more than basal half straight and parallel, rather broadly rounded in front; surface subshining, indications of reticulation obscure but usually visible at high magnification toward anterior or basal areas, punctures coarse, very close, deep, irregular in size in some specimens, interspaces usually equal to less than one-fourth diameter of a puncture; median line partly impunctate, not raised; glabrous.

Elytra 1.8 times as long as wide, 1.8 times as long as pronotum; outline as in *gracilis;* striae moderately impressed, punctures rather coarse, deep; interstriae as wide as striae, punctures moderately coarse, close, confused, their anterior margins elevated into fine, crenulate, transverse ridges of variable height (this character approached in allied species, but not to this degree). Declivity convex, steep; striae narrowly, deeply impressed, punctures somewhat obscure; interstriae about twice as wide as striae, armed by fine, confused tubercles. Vestiture confined to declivity, scalelike.

MALE.— Similar to female except slightly stouter, and last visible abdominal sternum medially impressed and pubescent.

TYPE LOCALITY.— New Mexico.

TYPE MATERIAL.— The female holotype, male allotype, and 18 paratypes were mounted on cards all on one pin bearing the label "New Mexico, F. H. Snow." One paratype in the Canadian National Collection labeled "Las Vegas Hot Springs, New Mexico, 7000 ft., Aug. '82, F. H. Snow" may be from the same series. One paratype from each of the following Arizona localities is labeled: Hanagan Camp Ground, Greenlee Co., 12-VII-68, D. E. Bright; Santa Catalina Mts., 5-VIII-68, D. E. Bright.

The holotype, allotype, and 18 paratypes are in my collection; the three remaining paratypes are in the Canadian National Collection.

Scolytus torulus, n. sp.

This species is distinguished from *dimidiatus* Chapuis by the smaller average size, by the subvertical, somewhat convex abdominal sternum 2, by the absence of a tuft of hair on sternum 2 immediately posterior to the spine, by the very different male frons, and by other characters described below.

MALE.— Length 2.4 mm (paratypes 2.0-2.4 mm), 2.1 times as long as wide; color very dark brown to black, elytra slightly lighter.

Frons rather weakly convex above, a distinct, moderately deep, transverse impression just above epistoma, deepest in median area, a distinct but weak, rounded, median elevation immediately above impressed area; surface strongly reticulate above, more shining and obscurely aciculate in impressed area, punctures fine, rather deep, sparse in median area, more numerous laterally; vestiture of fine hair on margins and impressed area, a few of them rather long.

Pronotum as in *dimidiatus* except punctures in lateral areas considerably larger.

Elytra 1.1 times as long as wide, 1.2 times as long as pronotum; surface similar to *dimidiatus* but much more finely punctured, few to many longitudinal lines or striations sometimes present. Sparse setae shorter and much stouter than in *dimidiatus.*

Sternum 2 subvertical, moderately convex, spine similar to *dimidiatus* but smaller; surface dull, very coarsely, deeply, closely punctured; sterna 3-5 similar but more finely punctured; vestiture of very fine, short hair, without a specialized tuft posterior to spine on 2.

FEMALE.— Similar to male except frons without impression or elevation, not strigose, vestiture similar to but finer and about one-third as abundant as in *dimidiatus* female; spine on sternum 2 about half as large as in male.

TYPE LOCALITY.— Rincón de Osa, Puntarenas, Costa Rica.

TYPE MATERIAL.— The male holotype, female allotype, and 10 paratypes were taken at the type locality on 11-VIII-66, 30 m, No. 72, from a leguminous tree, by me.

The holotype, allotype, and paratypes are in my collection.

Scolytus laetus, n. sp.

This species is distinguished from *torulus* Wood by the flattened sternum 2 which is much more finely, sparsely punctured, with longer, more abundant hair, and by characters of the frons described below.

Male.— Length 2.4 mm (paratypes 2.4-2.5 mm), 2.4 times as long as wide; color very dark brown.

Frons as in *torulus* except elevation wider, area above elevation more distinctly, more broadly impressed, vestiture on lateral margins more abundant, much longer.

Pronotum and elytra as in *torulus.*

Sternum 2 vertical, almost flat, surface dull, punctures small, not clearly evident, spine as in *torulus,* vestiture much longer, some setae as long as spine.

Female.— Similar to male except frons as in female *torulus* but with vestiture slightly more abundant and longer, particularly in lower areas; sternum unarmed, spine absent, vestiture finer, more abundant.

Type Locality.— Forty-eight km or 30 miles N Rosamorada, Nayarit, Mexico.

Type Material.— The male holotype, female allotype, and three male paratypes were taken at the type locality on 15-VII-65, 1000 m, No. 257, from *Inga paterno,* by me.

The holotype, allotype, and paratypes are in my collection.

Scolytodes amabilis, n. sp.

In general body features, this species is very similar to *clusiavorus* Wood, but the female frons is much more similar to *volcanus* Wood. It is distinguished from those species as indicated below.

Female.— Length 1.6 mm (paratypes 1.4-1.6 mm), 2.5 times as long as wide; color very dark brown, almost black.

Frons essentially convex, with a very shallow, subconcave area on median third just below upper level of eyes, this impression continued on median fifth as an abrupt, shallow sulcus to epistoma, median half of lateral areas bordering sulcus with numerous beadlike granules, remaining areas somewhat dull, with fine punctures; surface of sulcus shining, almost smooth; rather sparse vestiture limited to margins, of fine, long hair, those on dorsal margin attaining level of antennal insertion, shorter laterally and below.

Pronotum and elytral outlines as in *clusiacolens* Wood; pronotum surface reticulate, punctures as in *clusiavorus;* strial and interstrial punctures similar to but slightly larger than in *clusiavorus.* Strial setae almost obsolete; interstrial setae almost obsolete on even-numbered interstriae, fine, rather short, and widely spaced on odd-numbered interstriae.

Male.— Similar to female except frons convex, reticulate, vestiture very sparse, short, inconspicuous.

Type Locality.— Mt. Tzontehuitz, Chiapas, Mexico.

Type Material.— The female holotype, male allotype, and 15 paratypes were taken at the type locality on 29-V-69, at 3000 m, by D. E. Bright. Twenty-one paratypes bear the same data except 23-VI-69; two of them were taken from *Quercus* sp.

The holotype, allotype, and most of the paratypes are in the Canadian National Collection; the remaining paratypes are in my collection.

Scolytodes obesus, n. sp.

This species is distinguished from the remotely related *immanus* Wood by the smaller size, by the stouter body form, by the pair of carinae on the female frons, and by other characters.

Female.— Length 1.8 mm, 2.1 times as long as wide; color yellowish brown, anterior third of pronotum darker.

Frons shallowly, broadly concave from level of antennal insertion to upper level of eyes (upper area concealed by pronotum), surface smooth and shining except subreticulate near margins; epistomal area from margin to level of antennal insertion longitudinally divided into equal thirds by a pair of rather strongly elevated carinae; premandibular epistomal lobe large, conspicuous, pubescent; vestiture mostly confined to margins of upper half of frontal area, consisting of a row of long, subplumose setae, longest setae equal to about one-half to two-thirds distance between eyes.

Pronotum 0.97 times as long as wide; widest near base, sides weakly, arcuately converging on basal two-thirds, rather broadly rounded in front; anterior third moderately declivous, finely asperate; posterior areas reticulate, very finely, rather closely punctured. Glabrous except for an occasional coarse seta on asperate area.

Elytra 1.15 times as long as wide, 1.25 times as long as pronotum; sides almost straight on basal half, slightly wider at base of declivity, rather broadly rounded behind; disc confined to basal half; striae not impressed, punctures small, rather shallowly impressed, spaced by distances equal to diameter of a puncture; interstriae four times as wide as striae, smooth, shining, punctures small to minute, weakly impressed; interstriae 10 weakly carinate to level of sternum 5. Declivity convex, moderately steep; sculpture as on disc. Vestiture of sparse, moderately long bristles on odd-numbered interstriae.

Protibia slender, lacking minute tooth on posterior face near tarsal insertion.

Type Locality.— Barro Colorado Island, Panama Canal Zone.

Type Material.— The female holotype was taken at the type locality on 7-VIII-67, L. and C. W. O'Brien.

The holotype is in my collection.

Scolytodes lepidus, n. sp.

This species is distinguished from *amoenus* Wood by the slightly larger average size, by the slightly larger elytral punctures, by the presence of a few elytral setae, particularly along sides, and by the very different female frons.

Female.— Length 2.0 mm (paratypes 1.8-2.3 mm), 2.2 times as long as wide; color dark brown, base of pronotum usually pale.

Frons broadly flattened from epistoma to vertex, almost smooth, upper half and sides below coarsely, closely punctured and pubescent, median third on lower half slightly elevated, smooth, shining, impunctate, glabrous; vestiture long, moderately abundant, more widely distributed than in *amoenus*.

Pronotum 1.0 times as long as wide; as in *amoenus* except discal area reticulate (smooth to subreticulate in *amoenus*) and moderately pubescent at lateral margins (almost glabrous in *amoenus*).

Elytra 1.2 times as long as wide, 1.3 times as long as pronotum; as in *amoenus* except strial and interstrial punctures larger, more completely confused and lateral areas with sparse setae (entirely glabrous in *amoenus*).

Male.— Similar to female, with frons similar to male *amoenus* except more coarsely punctured, more protuberant in median area, with no granules.

Type Locality.— Thirty-three km or 21 miles N Juchitlan, Jalisco, Mexico.

Type Material.— The female holotype, male allotype, and 25 paratypes were taken at the type locality on 3-VII-65, at 1300 m, No. 177, from *Ficus*, by me, from the same branches that contained the type series of *amoenus*.

The holotype, allotype, and paratypes are in my collection.

Scolytodes genialis, n. sp.

This species is distinguished from *lepidus* Wood by the absence of punctures in the asperate area of the pronotum and by the much finer punctures on the pronotal disc and on the elytra.

Female.— Length 1.8 mm (paratypes 1.8-2.1 mm), 2.3 times as long as wide; color light brown, anterior half of pronotum darker.

Frons as in *lepidus* except vestiture finer, very slightly shorter. Pronotum as in *lepidus* except punctures very fine, shallow. Elytra as in *lepidus* except strial punctures fine, shallow, in definite rows, interstrial punctures very small, confused, striae 1 not impressed on declivity, vestiture on sides of elytra minute.

Type Locality.— Laguna Santa María, Nayarit, Mexico.

Type Material.— The female holotype, male allotype, and six paratypes were taken at the type locality on 7-VII-65, at 900 m, No. 197, from *Ficus* with yellow bark, by me. Four paratypes are from 24 km or 15 miles S Mazamitla, Jalisco, Mexico, 22-VI-65, 2500 m, No. 97, *Ficus* with yellow bark, by me.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes concentralis, n.sp.

This species is distinguished from *quercinus* Wood by the concentric, carinate pronotal asperities, by the more strongly impressed frons, by the greatly reduced elytral punctures, and by the wider elytral scales.

Female.— Length 1.0 mm (paratypes

1.0-1.2 mm), 2.6 times as long as wide; color dark brown.

Frons rather strongly concave on median two-thirds of area below upper level of eyes, surface subrugose, with sparse granules except almost smooth on lower half of concavity; vestiture short, sparse. Antennal scape as wide as long, as long as pedicel, bearing a small tuft of long hair; club about as in *quercinus*.

Pronotum 0.73 times as long as wide; outline as in *quercinus;* summit at middle; anterior slope on median third armed by six concentric, uniform, transverse carinae, other asperities absent, carina 1 submarginal, 6 at summit; posterior areas shining, almost smooth, punctures almost obsolete. Vestiture consisting of a row of scales posterior to each of first five carinae, and rather sparse, coarse hair in remaining areas.

Elytra 1.8 times as long as wide, 2.4 times as long as pronotum; outline as in *quercinus;* striae not impressed, punctures small, shallow; interstriae almost smooth, about twice as wide as striae, punctures almost obsolete; surface usually covered by a thin incrustation. Declivity convex, steep, sculpture as on disc but punctures even more obscure. Vestiture mostly abraded, consisting of widely spaced, short, interstrial scales, each scale one and one-half to two times as long as wide.

MALE.— Length 0.8 mm; similar to female except smaller, slightly stouter; frontal concavity not as deep; pronotal asperities not fused or clearly concentric.

TYPE LOCALITY.— Ten km or 6 miles SE Totolapan, Oaxaca, Mexico.

TYPE MATERIAL.— The female holotype, male allotype, and 24 paratypes were taken at the type locality on 21-VI-67, 1000 m, No. 73, from a leguminous roadside shrub with a yellow flower that was presumed to be *Cassia* sp., by me.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes tumidulus, n. sp.

This species is distinguished from the distantly allied *graniticus* Wood by the different female frons, by the smaller elytral scales, and by the very different male declivity as described below.

MALE.— Length 1.7 mm (paratypes 1.5-2.0 mm), 2.2 times as long as wide; color very dark brown.

Frons flattened on lower two-thirds, with small concavity on median fifth, ascending slightly to epistomal margin, convex above; subshining and almost smooth on flattened area, more coarsely punctate-granulate above; vestiture confined to epistomal area and to convex area.

Pronotum similar to *graniticus* except anterior margin narrowly rounded and armed by six teeth and posterior areas rather strongly reticulate.

Elytra 1.3 times as long as wide; sides straight and parallel on basal three-fourths, rather abruptly rounded, then broadly rounded behind; striae not impressed, punctures small, moderately deep, spaced by distances equal to diameter of a puncture; interstriae three times as wide as striae, almost smooth, punctures minute, granulate, uniseriate except confused near declivity. Declivity with basal margin abrupt, basically convex except upper half flattened to striae 4, a moderate bulla just below middle from interstriae 2-4; strial punctures smaller and not as deep as on disc, closer, in indistinct rows, of same size and shape as confused interstrial granules, interstrial punctures obsolete; bulla covered by same surface sculpture as elsewhere. Vestiture of interstrial rows of scales, each slightly longer than wide on disc except scales confused, more abundant, much longer, and more slender at base of declivity; declivity glabrous; rows of fine, recumbent strial hair on disc.

FEMALE.— Similar to male except frons broadly, shallowly concave from epistoma to well above eyes, vestiture on upper area slightly more abundant (less abundant and shorter than in *graniticus*); anterior margin of pronotum more broadly rounded, unarmed; declivity convex, sculpture as on disc except strial punctures obsolete; rows of interstrial scales continued to apex, each scale equal in length to three-fourths distance between rows, more closely spaced within a row, each about three to four times as long as wide.

TYPE LOCALITY.— Highway 120, 129 km NE San Juan del Río, Queretaro, Mexico.

TYPE MATERIAL.— The male holotype, female allotype, and 27 paratypes were taken at the type locality on 9-VI-71, at

2500 m, from mistletoe on oak, by D. E. Bright.

The holotype, allotype, and most of the paratypes are in the Canadian National Collection; the remaining paratypes are in my collection.

Thysanoes tuberculatus, n. sp

This species is distinguished from *granulifer* Wood by the smaller size and by the very different elytral declivity as described below.

Male.— Length 1.8 mm, 2.7 times as long as wide; color rather dark yellowish brown.

Frons and pronotum as in *granulifer* and *berchemiae* Blackman.

Elytra 1.6 times as long as wide; disc as in *granulifer* except granules slightly larger. Declivity steep, convex; striae 1 and 2 with punctures minute, visible almost to apex; suture slightly elevated, with a row of small granules on basal half; interstriae 2 with two or three tubercles on less than basal fourth, broadly impressed below and entirely devoid of punctures and granules; interstriae 3 moderately elevated on middle third and armed with a row of six to eight rather coarse tubercles, lower third without punctures or granules; lateral interstriae each with a row of tubercles on basal area but none of them attaining normal apex for these interstriae. Vestiture of rows of interstrial scales, scales on disc largely abraded, little if any longer than wide, longer at base of declivity; those on 3 up to three times as long as on disc and four times as long as wide, slightly shorter on other interstriae; declivital interstriae 2, 4, lower two-thirds of 1, and lower half of 3 glabrous.

Type Locality.— Eighty-five km or 53 miles S Valle Nacional, Oaxaca, Mexico.

Type Material.— The male holotype was taken at the type locality on 24-V-71, at 3300 m, D. E. Bright.

The holotype is in the Canadian National Collection.

Pityokteines mystacinus, n. sp.

This species is distinguished from *minutus* (Swaine) by the smaller size, by the very different ornamentation of hair on the female frons, by the finer pronotal and elytral punctures, and by other characters. It probably is much more closely related to *lasiocarpi* (Swaine).

Female.— Length 2.1 mm (paratypes 1.7-2.1 mm), 3.0 times as long as wide; color brown.

Frons similar to *lasiocarpi* except more broadly convex, surface not as smooth, somewhat dull, punctures average smaller and, on lower third, becoming almost obsolete; vestiture on lower third abundant, rather long, epistomal brush very broad, rather dense; setae on upper half of frontal area sparse, short. Antennal club almost as in *lasiocarpi*.

Pronotum as in *lasiocarpi* except anterior margin more narrowly rounded; vestiture uniformly short as in *lasiocarpi*. Elytra as in *lasiocarpi* except punctures on disc slightly larger, very slightly more confused on basal half, and declivital striae 1 more strongly impressed, with punctures on striae 1 slightly larger, subapical transverse elevation at apex of sulcus more distinct (but still rather obscure); position, number, and size of tubercles as in *lasiocarpi*. Vestiture similar in abundance, but very slightly longer than a *lasiocarni*.

Male.— Similar to female except upper half of frons more strongly convex, vestiture on lower third greatly reduced in abundance and length; elytral declivity with sulcus slightly deeper (about as in male *lasiocarpi*) but narrower.

Type Locality.— Mount Rainier National Park, Washington.

Type Material.— The female holotype, male allotype, and three female paratypes were taken at the type locality on 21-VIII-62, silver fir, D. E. Bright.

The holotype, allotype, and one paratype are in the Canadian National Collection and two paratypes are in my collection.

Ips pilifrons thatcheri, n. subsp.

This geographical race of *pilifrons* is distinguished from *p. pilifrons* Swaine, of northern Colorado, by the characters of the frons described below. Both subspecies are replaced throughout all of Utah by *p. utahensis* Wood in which frontal characters are entirely different. The following comparisons are based on females having the maximum frontal elevation and pilosity for their race; occasional specimens of *p. pilifrons* almost overlap the maximum development of *p. thatcheri.*

Female.— Length 4.6 mm (paratypes 3.9-4.9 mm), 2.5 times as long as wide; color very dark brown.

Frons similar to *p. pilifrons* except less strongly, less extensively elevated, elevation occupying lower 80 percent of median distance from epistoma to upper level of eyes (115 percent in *p. pilifrons*) and pubescent area occupying less than 50 percent of median area between eyes (80 percent in *p. pilifrons*); lateral areas much more sparsely, more finely granulate than in *p. pilifrons*. Pronotum, elytra, and other features essentially as in *p. pilifrons.*

Male.— Similar to male *p. pilifrons* except frontal vestiture less abundant and shorter, particularly along epistoma.

Type Locality.— Mt. Wheeler, Nevada.

Type Material.— The female holotype, male allotype, and 48 paratypes were taken at the type locality on 10-VIII-74, at 10,000 ft., from *Picea engelmanni*, by me.

The holotype, allotype, and paratypes are in my collection.

This subspecies is named for Dr. T. O. Thatcher who discovered it more than 30 years ago.

Araptus attenuatus, n. sp.

This species is distinguished from *placatus* Wood by the much coarser strial punctures, by the much longer female frontal vestiture, and by other characters cited below.

Female.— Length 1.6 mm (paratypes 1.4-1.6 mm), 3.0 times as long as wide; color dark brown.

Frons feebly convex, flattened on median half in some specimens; subshining, rather finely, closely punctured in peripheral areas, central area minutely irregular, often with a few punctures; a weak median carina on lower half; vestiture of fine, long, white, subplumose setae in punctured area at sides and above, longest setae equal to two-thirds diameter of frons, shorter toward epistoma.

Pronotum 1.2 times as long as wide; as in *placatus* except anterior margin more narrowly rounded, posterior areas more distinctly reticulate, with punctures almost twice as large; minute setae present on disc.

Elytra 1.8 times as long as wide, 1.6 times as long as pronotum; similar to *placatus* except strial punctures almost twice as large, declivity more narrowly convex, interstriae 2 not impressed, 1 more feebly elevated. Minute strial setae visible on posterior half of disc and declivity except 1 and 2, interstrial setae confined to declivity, absent on 2, similar to *placatus* except usually finer.

Male.— Similar to female except frons more distinctly convex, punctures subrugose, obscurely acicutate, a distinct, subtuberculate, median prominence at upper level of eyes and continuing toward vertex, its summit transversely etched.

Type Locality.— Forty-eight km or 30 miles W Bajia de los Angeles, Baja California Norte, Mexico.

Type Material.— The female holotype, male allotype, and four paratypes were taken at the type locality on 31-III-74, Hopk. 58650, by M. M. Furniss, from host plant No. 88. Twenty-two paratypes are from 32 km or 20 miles N Punta Prieta, Baja California Norte, Mexico, 29-III-73, *Pedialanthus macrocarpus*, J. Doyen.

The holotype, allotype, and several paratypes are in my collection; two paratypes are in the Canadian National Collection; the remaining paratypes are in the University of California (Berkeley) Collection.

Araptus fossifrons, n. sp.

This common species was thought to be *foveifrons* (Schedl) until the type of Schedl's species became available for study; however, this species has the elytral punctures much finer and the declivital sulcus much more weakly impressed.

Male.— Length 2.2 mm (paratypes 1.8-2.4 mm), 2.5 times as long as wide; color rather dark reddish brown.

Frons as in *foveifrons* except lower area more finely punctured. Elytral disc with punctures much finer, interstrial punctures usually more widely spaced (variable). Elytral declivity with striae 1 rather strongly impressed, interstriae 2 not impressed, with a row of punctures. Vestiture as in *foveifrons.*

Female.— Similar to male except frons weakly convex, a weak median carina from vertex to epistoma, surface closely, rather coarsely punctured, with fine abundant, moderately long hair uniformly distributed from epistoma to above eyes; frons concealed in only available female of *foveifrons*.

Type Locality.— Lago Amatitlan, Guatemala.

Type Material.— The male holotype, female allotype, and 48 paratypes were taken at the type locality on 10-VI-64, 700 m, No. 702, from the fruiting body of a climbing (Cucurbitaceae) vine, by me. Other paratypes were taken in Mexico as follows: 9 at 3 km (2 miles) SE Acatlan, Puebla, 15-VI-67, 1500 m, No. 37; 17 at 9 km (12 miles) SE Oaxaca, Oaxaca, 18-VI-67, No. 57; 4 from 24 km (15 miles) W Armeria, Colima, 30-VI-65, 30 m, No. 141; 9 from 1 km N Atenquique, Jalisco, 24-VI-65, 1000 m, No. 115; 2 from 8 km (5 miles S Atenquique, Jalisco, 25-VI-65, 1000 m, No. 115A; 3 from 8 km (5 miles) W Juchitlan, Jalisco, 2-VII-65, 1000 m, No. 174; 14 from 24 km (15 miles) S Mazamitla, Jalisco, 22-VI-65, 2500 m, No. 96; 13 from Tuxpan, Jalisco, 23-VI-65, 1300 m, No. 99; 3 from 8 km (5 miles) N Ruiz, Nayarit, 14-VII-65, 100 m, No. 245; all from fruiting pods of climbing vines or a small tree, by me.

The holotype, allotype, and paratypes are in my collection.

Amphicranus parilis, n. sp.

This species is distinguished from *filiformis* Blandford by the much smaller size, by the absence of minute crenulations on the base of the pronotal disc, and by differences in the elytral declivity indicated below.

Male.— Length 2.0 mm, 4.0 times as long as wide; color pale yellowish brown, elytral declivity brown.

Frons and pronotum as in *filiformis* except as noted in diagnosis. Elytra as in *filiformis* except less strongly explanate, sutural emargination only slightly deeper than wide (twice as deep as wide in *filiformis*), declivital spine 2 smaller, less strongly pointed.

Type Locality.— Six km or 4 miles W Tepic, Nayarit, Mexico.

Type Material.— The male holotype was taken at the type locality on 13-VII-65, 1000 m, No. 240, from a tree branch, by me.

The holotype is in my collection.

Corthylus cecropii, n. sp.

This abberrant species is distinguished from all other species in the genus by the small antennal club, without sutures, by the absence of female pronotal asperities, and by the minute to obsolete punctures of the pronotum and elytra.

Female.— Length 2.4 mm (paratypes 2.0-2.5 mm), 2.3 times as long as wide; color black.

Frons uniformly, deeply concave from eye to eye, from epistoma to vertex; surface densely, uniformly, very finely punctured over entire surface; vestiture very fine, rather abundant, uniformly rather short over concave area, margin above eyes with a dense row of very long hair, a small tuft of longer hair at level of antennal insertion on lateral half. Antennal club 1.6 times as long as wide; asymmetrically obovate, aseptate, entire surface minutely pubescent; posterior face with a small tuft of hair extending about half of club length beyond apex.

Pronotum 1.1 times as long as wide; sides weakly arcuate on posterior half, broadly rounded in front, a distinct, submarginal, transverse constriction; anterior margin unarmed; summit indefinite, near middle; asperities absent; surface reticulate, anterior half with sparse, minute granules, posterior half with sparse minute punctures. Acute lateral margins more strongly developed than in other species. Glabrous.

Elytra 1.3 times as long as wide, 1.2 times as long as pronotum; sides almost straight and parallel on basal two-thirds, obtusely subangulate behind; disc reticulate, a few obscure, irregular lines indicated, punctures minute, mostly obsolete, apparently confused. Declivity occupying slightly more than posterior third, rather steep, convex; sculpture as on disc, except a few irregularly placed fine granules usually present. Vestiture confined to declivity, consisting of sparse, short, fine bristles apparently on odd-numbered interstriae.

Male.— Similar to female except frons convex, a distinct, transverse impression above epistoma, surface smooth, shining, impunctate; anterior margin of pronotum distinctly produced toward median line and armed by two slender teeth; anterior slope of pronotum much steeper, asperate.

TYPE LOCALITY.— Tapanti, Cartago, Costa Rica.

TYPE MATERIAL.— The female holotype, male allotype, and 15 paratypes were taken at the type locality on 24-X-63, 1300 m, No. 242, from fallen *Cecropia peltata* petioles, by me. Eight paratypes are from Turrialba, Cartago, Costa Rica, 5-VII-63, 700 m, No. 19, *Cecropia petioles*, by me. Three paratypes are from 6 km S San Vito, Puntarenas, 13-III-68, H. Hespenheide. Three specimens not included in the type series are from El Laurel (Experiment Station), 12 km SW Caracas, Venezuela, 1-V-70, 1300 m, No. 475, *Cecropia* petioles, by me.

The holotype, allotype, and paratypes are in my collection.

GENETICS, ENVIRONMENT, AND SUBSPECIES DIFFERENCES: THE CASE OF *POLITES SABULETI*

(Lepidoptera: Hesperiidae)

Arthur M. Shapiro[1]

ABSTRACT.— *Polites sabuleti* is an example of an insect having a univoltine, monophenic high-elevation subspecies and a multivoltine lowland one that produces similar phenotypes only in cold weather. When reared under conditions that induce the warm-weather phenotype in lowland stocks, the montane subspecies *P. s. tecumseh* continues to produce its usual phenotype, indicating that it has become genetically fixed.

One variant of the persistent "genetics-environment" duality in biology concerns the nature of subspecies differences. The problem, as it applies to butterflies, was well summarized in Klots's (1951) discussion of geographic variation:

> To what degree much of the recorded geographic variation is a matter of temperature and humidity differences is something which we can only infer. In *Papilio glaucus* . . . spring specimens tend to be small and pale. . . . As we go northward we find that in central Canada, where there is only one generation a year, the whole population looks similarly small and pale. In Canada this population has been named as a geographic subspecies, "*canadensis*," i.e. a part of the species limited to a certain area and showing distinctive characteristics. The temptation is strong to attribute the whole thing to lowered temperatures alone. But suppose we brought a batch of eggs of *canadensis* down to Florida, and reared the butterflies in the conditions under which the very large, richly colored subspecies *australis* develops there. Would our *canadensis* eggs develop as *australis* . . . or would they develop into the same small pale specimens that their parents were?

Twenty-three years later Ehrlich, Holm, and Parnell (1974) could only write that

> many butterflies have spring generations that are smaller and darker than their summer generations, the difference presumably being due to the seasonal variation in the environment. However, in some northern parts of their range, [they] have only a single summer generation, which is small and dark and resembles the spring generation of southern localities. In the northern populations, the individuals are presumed to have genotypes that produce the dwarfing and darkening. *Although the critical transfer experiments have not been done,* the greater constancy of the northern forms in the face of environmental changes supports these presumptions [emphasis added].

The same problem was recognized in plants as far back as the 1920s, in the classic work of Turesson (1922, 1925, 1929) later brilliantly expanded by Clausen, Keck, and Hiesey (1940, 1947, 1948, and other papers). This work firmly established the concept of the ecotype in plant ecology and genetics, a concept more or less readily generalizable to animals in cases like those discussed by Klots and Ehrlich et al. Turesson and Clausen et al. were able, by transplant experiments, to separate phenotypic variation produced directly by the physical environment from that produced indirectly through the selection of climatically adapted genotypes. This paper is the second of a series reporting on analogous studies of North American Lepidoptera.

THE SUBSPECIES OF POLITES SABULETI

Situations of the sort described above are not limited to populations separated by latitude; many Lepidopterans—like the plants studied by Clausen and his colleagues—have *altitudinal* variants, often described taxonomically at the subspecies level, and these are especially interesting because of the short ground distances between the high- and low-elevation populations and the possibility of investigating the nature of their contacts, if any.

Polites sabuleti Boisduval is a small, largely tawny skipper (Hesperiidae), widely distributed in western North America. Three named subspecies occur in California: *P. s. sabuleti*, *P. s. tecumseh* Grinnell, and *P. s. chusca* Edwards. The last is a very pale desert population and has not been examined in this study. *P. s. sabuleti* and *P. s. tecumseh* are parapatric in northern and central California, occurring at low and high elevations respectively.

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P. s. sabuleti is very widespread on sandy soils, in saline and alkaline marshlands, and in urban vacant lots. It is usually closely associated with its normal larval host, alkali grass (*Distichlis spicata* [L.] Greene, Gramineae), but may breed occasionally on Bermuda grass (*Cynodon dactylon* [L.] Pers.), an introduced lawn grass and weed. *P. s. sabuleti* is strongly multivoltine at sea level, with possibly as many as five generations a year. The flight season is very long, ranging from late March-April to mid- or late November at Sacramento and Suisun City, California.

P. s. tecumseh occurs in subalpine meadows that become dry in summer, and in alpine fell-fields in the high Sierra Nevada. Its host plant is not known, but many collectors have noted an association with species of sedges (*Carex*, Cyperaceae). Tilden (1959) reports *P. s. tecumseh* flying from July to September in Yosemite National Park, which he interprets as indicating two broods. The more complete data given in Garth and Tilden (1963) do not support this interpretation, as there is no wide spread of dates within a given year at a single locality. Farther north, at Donner Pass (7,000 feet) there is no indication of more than one brood. Emmel and Emmel (1962) found it there from 19 June to 19 August, 1960; Shapiro found it at the same localities from 11 July to 24 August, 1973, and 18 July to 12 August, 1974. The condition of Donner Pass specimens does not suggest even a partial second brood. Like many montane butterflies, *P. s. tecumseh* emerges later at higher elevations; thus, at 10,000 feet it flies mainly in August and into very early September.

As with the altitudinal subspecies of *Phyciodes campestris* Behr (Nymphalidae) previously studied (Shapiro, 1975a), those of *Polites sabuleti* are separated by a zone in which neither seems to occur. At the latitude of Sacramento, *P. s. sabuleti* is unknown as a breeding resident above 1,500 feet and *P. s. tecumseh* is unrecorded below 5,000 feet. Tilden (1959) confuses the matter by indicating that *P. s. sabuleti* extends much higher at Yosemite, but his data (given in Garth and Tilden, 1963) make it plain that this refers to the arid *east* slope only: the records are from Bridgeport (6,743 ft.) and Mono Lake (6,419 ft.). On the west slope the lowest Yosemite-area record of *P. s. tecumseh* is Gin Flat (7,036 ft.) and there are no records of *P. s. sabuleti* at all (although it is abundant on the floor of the San Joaquin Valley). The nature of the east-slope contacts has not been studied, but few habitats suitable for either subspecies occur on the abrupt Sierran escarpment.

Polites sabuleti tecumseh differs from summer *P. s. sabuleti* in being smaller, hairier, and more heavily marked, especially on the hindwing ventrally. The dark markings on this wing are often described as being a "colder," grayer color than in *P. s. sabuleti.* Although a series of 23 *tecumseh* from the vicinity of Donner Pass shows considerable variation, no seasonal pattern is apparent. In *P. s. sabuleti* from Sacramento and Suisun City (over 450 specimens examined) there is marked seasonal variation: March-May and September-November specimens are, on the average, smaller, darker, and hairier than summer ones, and some are superficially exceedingly similar to *P. s. tecumseh*, although there are minor (but fairly consistent) differences in certain details of the pattern. The phenotypes of wild specimens of both taxa are illustrated in Figures 1-3.

Experimental Methods and Results

Would stock of *P. s. tecumseh* reared under conditions that produce summer phenotypes of *P. s. sabuleti* produce the normal *tecumseh* phenotype, or would it be modified in the direction of the lowland, summer one? Ova were obtained from a female *tecumseh* collected at Donner Pass (7,000 ft.), 24 July 1974, and from two female *sabuleti* collected in a salt marsh at Suisun City, Solano County (10 ft.), 6 August 1974. The resulting progeny were reared side by side in plastic Petri dishes (5½" diameter X ¾") at comparable densities (5-8 larvae/dish) under continuous illumination from a 60w bulb at 25C (77F). All larvae were fed fresh cuttings of Bermuda grass (*Cynodon dactylon*), and mortality in both stocks was negligible. Thirty adult *P. s. sabuleti* (16 ♂ 14 ♀) and thirteen *P. s. tecumseh* (8 ♂ 5 ♀) were obtained. Continuous light was selected as a regime ecologically nonsignificant to both stocks but known

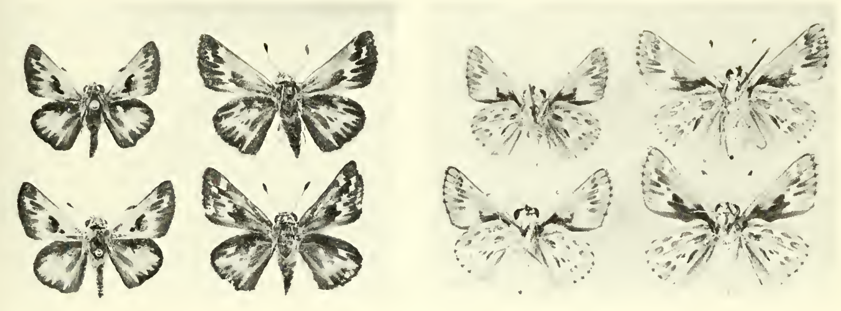

Fig. 1. Dorsal and ventral surfaces of summer specimens of *Polites sabuleti sabuleti* from the Central Valley of California.

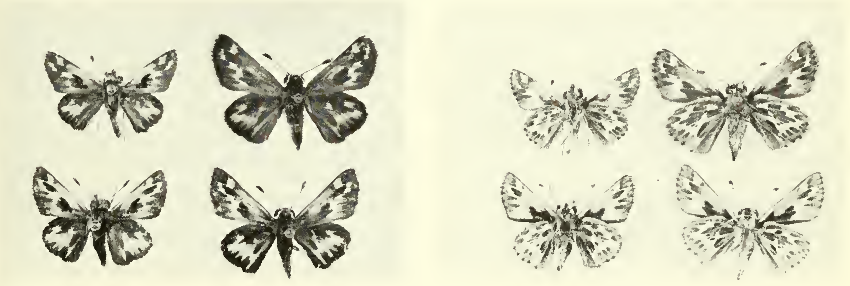

Fig. 2. Dorsal and ventral surfaces of early spring and late fall *P. s. sabuleti* from the Central Valley, approaching the phenotype of *P. s. tecumseh.*

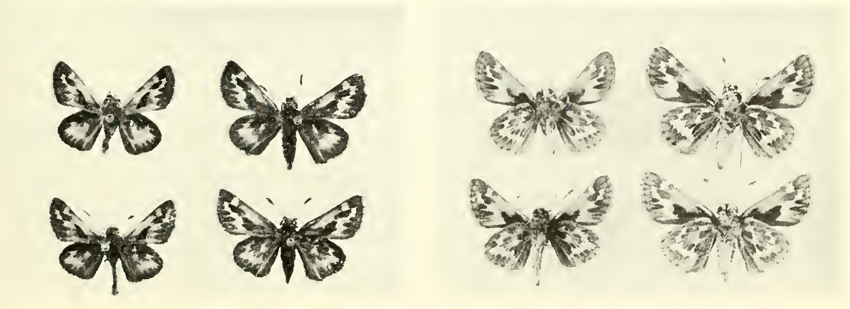

Fig. 3. Dorsal and ventral surfaces of *P. s. tecumseh* from Donner Pass, California (7,000 feet), July-August.

to inhibit diapause in *P. sabuleti* and related species.

The two stocks differed in several respects in the laboratory. First- and second-instar larvae of *P. s. sabuleti* were yellowish green; in the third instar they turned purplish brown; and thereafter they remained that color. *P. s. tecumseh* larvae were purplish brown throughout their development. At corresponding points in the life cycle the early stages of *P. s. sabuleti* were always larger than their high-altitude counterparts. The developmental rates of the two stocks differed very significantly, with little overlap: from egg to adult *P. s. sabuleti* took 39-76 days (weighted mean, 58.5 days) and *P. s. tecumseh*, 70-111 days (weighted mean, 86.0). No diapause was observed in either stock. Normally, high-elevation or -latitude stocks of Lepidoptera develop more rapidly than conspecific ones from more temperate climates when reared under uniform laboratory conditions; the reversal of this situation in *Polites sabuleti* is to my knowledge unique in Lepidopteran stocks in which diapause is not manifested in culture.

The developmental differences noted above were not mirrored in larval behavior or morphology. The adults, however, were obviously different and "true" to their normal phenotypes (Figs. 4, 5): nondiapaused *tecumseh* reared at high temperatures retained all of their distinguishing characters, including size. It thus appears that the complex of characters present as a developmental option in low-

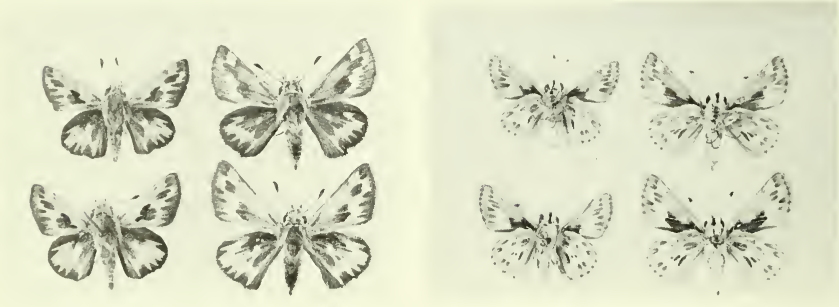

Fig. 4. Dorsal and ventral surfaces of representative bred *Polites sabuleti sabuleti;* continuous light, 25C.

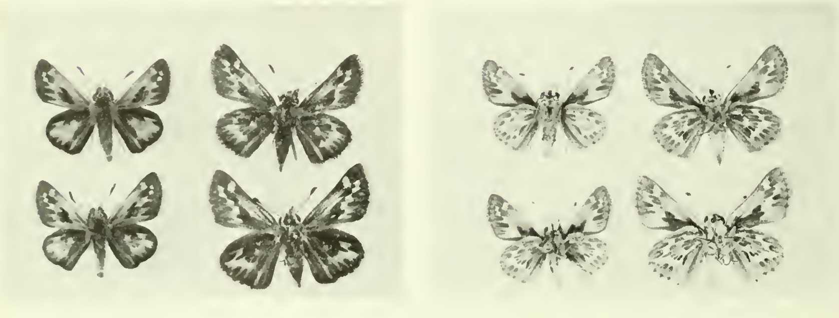

Fig. 5. Dorsal and ventral surfaces of representative bred *P. s. tecumseh*; same conditions as in Figure 4.

land, multivoltine populations is genetically fixed in *P. s. tecumseh*, confirming Ehrlich et al.'s prediction.

DISCUSSION

Three sets of "altitudinal subspecies" have now been investigated in butterflies, representing three different and quite unrelated families. They are *Pieris occidentalis* Reakirt and its alpine representative, familiarly (but incorrectly) known as *P. o. "calyce"* Edwards (Pieridae); *Phyciodes campestris* Behr and its montane subspecies *montana* Behr (Nymphalidae); and *Polites sabuleti*. The first two are discussed at length in Shapiro (1975a). Each species presents a picture different from the others.

Pieris occidentalis shows very little, if any, genetic differentiation of the univoltine, monophenic and bivoltine, diphenic populations of high and moderate elevations, respectively. The alpine stock retains the ability to produce an estival phenotype and to develop without diapause, and its own phenotype is indistinguishable from the vernal one produced downslope. Their mating behavior involves male aggregations on mountaintops, a behavior pattern conducive to gene flow, and in laboratory experiments no reproductive barriers have been found between uni- and bivoltine populations.

Phyciodes campestris shows a superficially similar picture, in that the high altitude subspecies *montana*, when reared under outdoor conditions at sea level, produces the foothill phenotype rather than its own. However, the cold-season phenotype of lowland populations is quite different from *montana*, and the ability to produce the *montana* phenotype appears to be restricted to high-elevation populations. In this case, then, phenotypic plasticity is not reciprocal, and the high-elevation population is genetically differentiated.

Polites sabuleti shows the highest degree of differentiation yet encountered. The possibility that it has achieved reproductive isolation (i.e., speciation) between high- and low-elevation populations cannot be discounted. Because of the difference in developmental time, no crosses between the stocks could be made. They are not known to intergrade anywhere, since the altitudinal discontinuity between them seems to run the length of the Sierra Nevada.

These experiments have been duplicated with a latitudinal subspecies pair—California *Pieris occidentalis* and its subspecies *P. o. nelsoni* Edwards from Fairbanks, Alaska (Shapiro, 1975b). Their phenotypic differences are clearly heritable, and the response of both phenotype and diapause to photoperiod has been observed in F_1 and F_2 hybrids.

Studies of the *Pieris occidentalis* and *P. napi L.* species complexes (Shapiro, 1975 c) strongly imply that univoltinism is evolutionarily derivative from multivoltinism, accompanying the successful invasion of increasingly rigorous climates. High-altitude and -latitude populations of widespread species are probably derived from lowland sources, as has been well documented for the Sierran alpine flora (Chabot and Billings, 1972). The overall picture emerging from these studies supports the suggestion that seasonal phenotypes of multivoltine populations may become fixed through selection of modifiers influencing thresholds of developmental expression ("genetic assimilation," Waddington, 1953). The somewhat unusual circumstances in *Phyciodes campestris montana* will be explored in another paper.

ACKNOWLEDGMENTS

Collection of livestock for this study was funded by Grant D-804 from the Committee on Research of the Academic Senate, U. C. Davis. Steven R. Sims, John H. Lane, and Adrienne R. Shapiro assisted in field work. Aspects of this research benefited from conversations from Michael Rosenzweig, William E. Bradshaw, and E. W. Jameson, Jr.

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LIFE HISTORY AND ECOLOGY OF *MEGARCYS SIGNATA* (PLECOPTERA: PERLODIDAE), MILL CREEK, WASATCH MOUNTAINS, UTAH[1]

Mary R. Cather[2] and Arden R. Gaufin[2]

Abstract.— During an investigation of some of the stoneflies (Plecoptera) of Mill Creek, Wasatch Mountains, Utah, *Megarcys signata*, a large omnivorous stonefly, was found to have a univoltine life history and a slow seasonal life cycle.

Temperature appears to affect the growth rate of *Megarcys signata*. Warmer stream temperatures accompany the acceleration of the growth rate, whereas cooler stream temperatures apparently retard the growth rate.

Periods of maximum absolute growth rate correspond with maximum carnivorous feeding from August to September and March to April. Chironomidae, Ephemeroptera, and Plecoptera, in that order, were the most abundant prey in the foreguts. Young nymphs ingested considerable amounts of diatoms, filamentous algae, and detritus but not as much animal matter as did older nymphs.

Megarcys signata was uniformly distributed throughout Mill Creek, except at the lowest station, where few nymphs were found.

Emergence occurred in May and June, the peak occurring in June. The mean size of females and males decreased as emergence progressed.

This report is part of an eighteen-month study of some of the stoneflies of Mill Creek, Wasatch Mountains, Utah. Because a detailed description of the study area and the methods and materials is given in another paper (Cather and Gaufin 1975, only a summary is included here.

Mill Creek Canyon is located 11 km southeast of Salt Lake City, Utah, in the Wasatch Mountains of the Middle Rocky Mountain Province. Six stations were selected along a 12 km length of the stream in the Wasatch National Forest with elevations ranging from 1,605 to 2,280 m. The sampling stations were numbered consecutively, Station I denoting the highest elevation. The three lower stations (1,605-1,785 m) are easily accessible all year, but the three upper stations (1,995-2,280 m) are accessible only in the summer and fall. Average minimum and maximum daily flows were 0.3 m^3/sec and 1.2 m^3/sec, respectively, during the study period. Depth averaged 11-45 cm, and current averaged 0.2-0.7 m/sec during the fall when measurements were taken. The substrate of the sampling area at all stations ranged from coarse sand to small cobbles. Minimum water and air temperatures recorded during adult emergence were 3 C and 9 C, respectively. Maximum water and air temperatures during this period were 13 C and 26 C, respectively. Water chemistry was similar at all stations. Dissolved oxygen ranged from 6.0 to 8.5 mg/l (70-120 percent saturation), calcium bicarbonate 109-189 mg/l, calcium carbonate 0-2.4 mg/l, pH 7.5-8.3, total hardness 100-340 mg/l, and conductivity 312-859 mhos/cm.

Methods and Materials

Nymphs of *Megarcy signata* were collected at least monthly from June 1971 to December 1972 at each of six stations. Additional nymphs were collected in spring 1973 for food habit studies. Handscreens of mesh sizes 7 and 9 sq/cm were used, the smaller handscreen being used during the majority of the study in an attempt to collect the smaller instars. An area of about 80 cm^2 of the stream bottom was disturbed in an attempt to collect at least 100 nymphs monthly. All nymphs were preserved in 80 percent ethanol.

Adults were collected weekly throughout the emergence period and biweekly during peak emergence using a sweep net and handpicking from vegetation, rocks, and bridges. All adults were preserved in 80 percent ethanol.

The interocular distance of all nymphs and adults was measured to the nearest 0.1 mm using an ocular micrometer in a dissecting microscope for determining growth rates and to see if the mean size of the adults decreased as emergence progressed. The nymphs were identified as males and females when possible.

Foregut analyses were conducted on 200 nymphs collected from the field. Nymphs were selected from an upper (I) and a

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[1] Study supported by Environmental Protection Agency Traineeship Grant No. 5T2-WP-542-03.

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lower (IV) station during each season (Station V had to be substituted for Station I during winter and spring). The method used followed Swapp (1972). All prey animals were enumerated and identified to order except where family or generic determination was possible. Three types of the family Chironomidae were recognized and designated as species a, b, and c (based on morphology of head capsule). These are discussed under results and discussion but are not separated in Table 1. All algae were determined to genus where possible. Percentage compositions of algae and detritus were estimated when present, and dominant items were recorded. A volume analysis was not conducted.

Identification of nymphs and adults followed Gaufin et al. (1966), and nomenclature followed Illies (1966) and Zwick (1973).

Results and Discussion

The only systellognathan stonefly present in Mill Creek in numbers large enough for analysis is *Megarcys signata.* This species exhibits a slow seasonal type of life cycle. Emergence and oviposition occur in May and June with hatching soon after. Small nymphs (0.5 mm interocular distance) appear in July at the lower stations. Nymphs of comparable size generally appear for the first time in August, September, and October at the upstream stations. Rapid growth occurs from August to emergence (Figs. 1a, b, c). The size

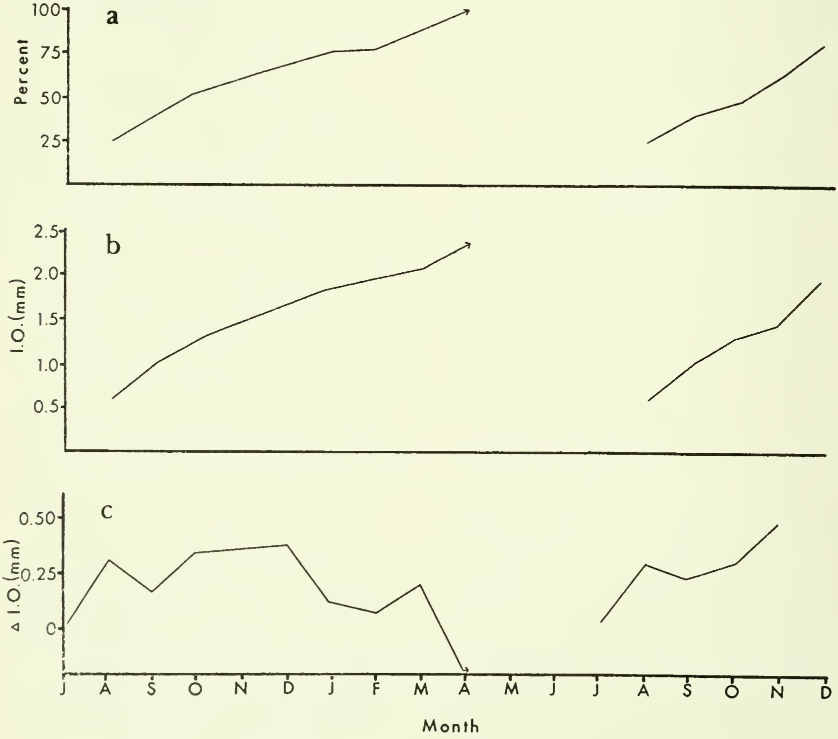

Fig. 1. Growth of *Megarcys signata.* Arrows indicate emergence. I. O. indicates interocular distance: (a) Monthly mean size as a percentage of total mean size at Station IV; (b) Monthly mean cumulative growth at Station IV; (c) Monthly mean absolute growth rate (data pooled from all stations). Δ indicates change in I. O. distance.

frequencies of nymphs and the mean cumulative growth at each station are shown in Figs. 2 and 3, respectively.

A comparison of the cumulative growth at all stations reveals that the most rapid growth occurs at the lowest (warmest) stations (Fig. 4). Thus, there seems to be a direct correlation between growth and temperature. Baumann (1967) found no direct correlation in this species in Mill Creek. Seasonally the most rapid growth occurs during the fall and early winter (September-January). Growth apparently slows, but does not stop, during the winter (January-March), increases from March to April, and then decreases from April to May, prior to emergence. Sheldon (1972) reported similar results in his study on the *Arcynopteryx* species complex he studied in California. However, Schwarz (1970) reported no growth at times during the winter in other Systellognatha. The correlation between growth and food habits will be discussed later.

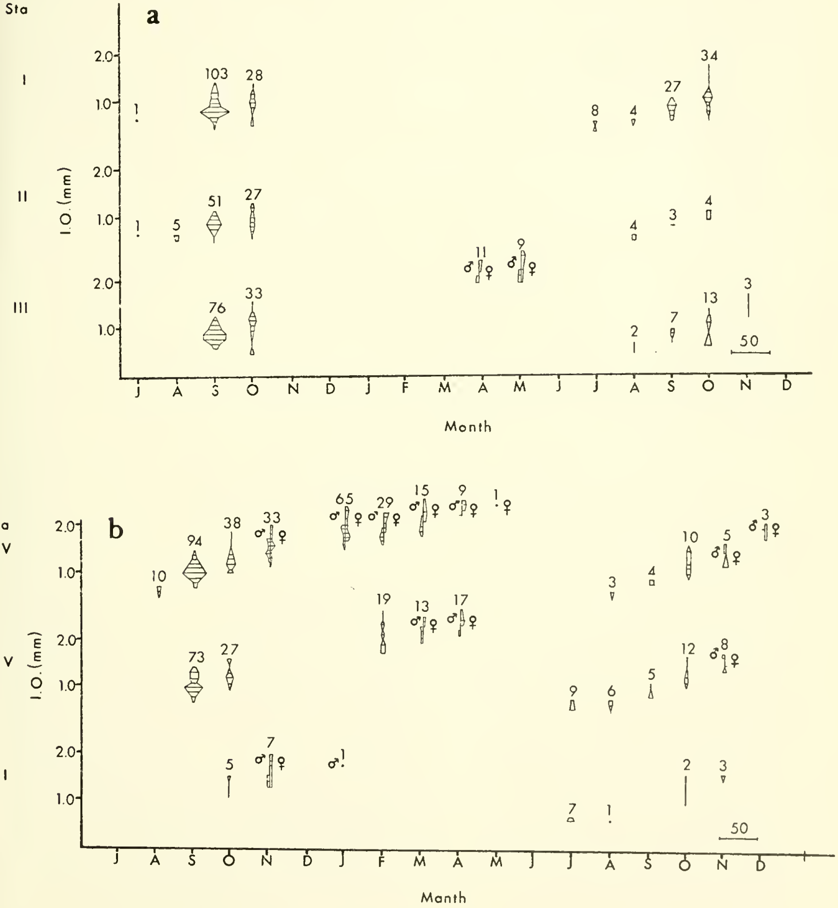

Fig. 2. Frequency distribution of nymphal size classes of *M. signata*. Number of individuals shown above each polygon; males and females as indicated: (a) Stations I, II, and III; (b) Stations IV, V, and VI.

Megarcys signata seems to show no preference for either the upstream or downstream stations. This species is evenly distributed throughout the stream except at Station VI. Here the substrate is almost entirely cemented. Where the water is deep enough for this large insect, the current is too slow; where the current is fast enough, the water is too shallow and the substrate too homogeneous. More individuals were collected at Station IV than at any other station.

The emergence of *M. signata* began in early May at the lower stations and lasted until late June at the higher stations (Fig. 5). Peak emergence was in June. Baumann (1967) found this species emerging from late April to mid-July in Mill Creek. Emergence is progressively later as the elevation increases. Baumann (1967), Hynes (1970), and Nebeker (1971) reported similar results. They were first collected at Stations III and V in early May, when the water tempera-

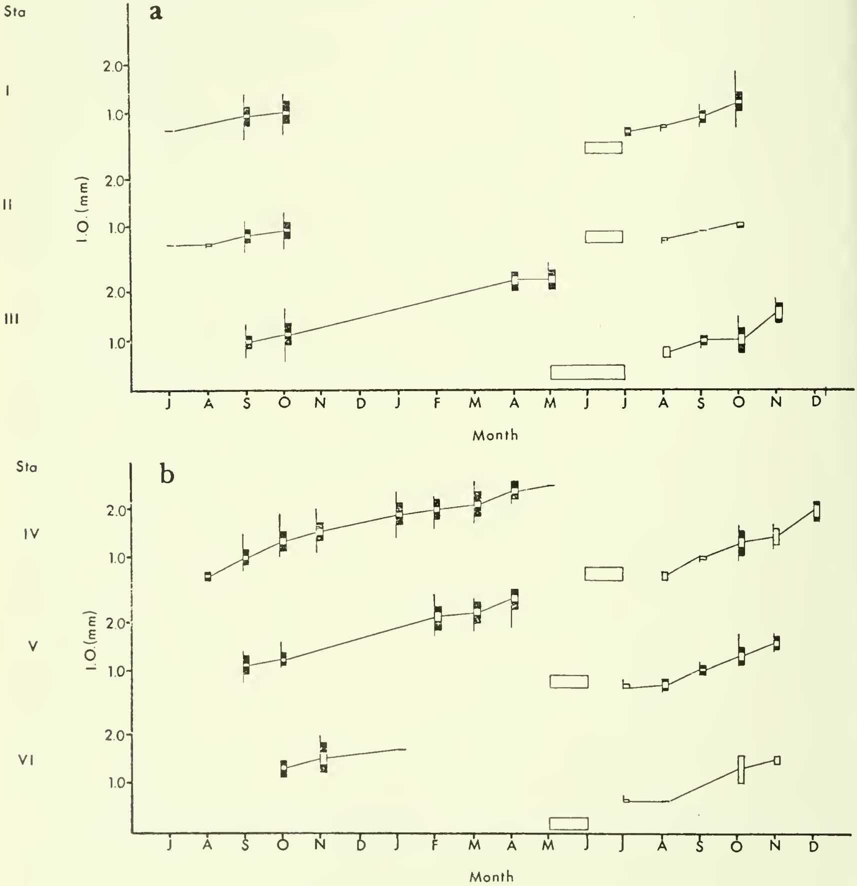

Fig. 3. Mean cumulative growth of nymphs of *M. signata*. Vertical line represents size range of nymphs; shaded area represents standard deviation; unshaded area represents standard error of the mean; solid line connects means; rectangle represents emergence period: (a) Stations I, II, and III; (b) Stations IV, V, and VI.

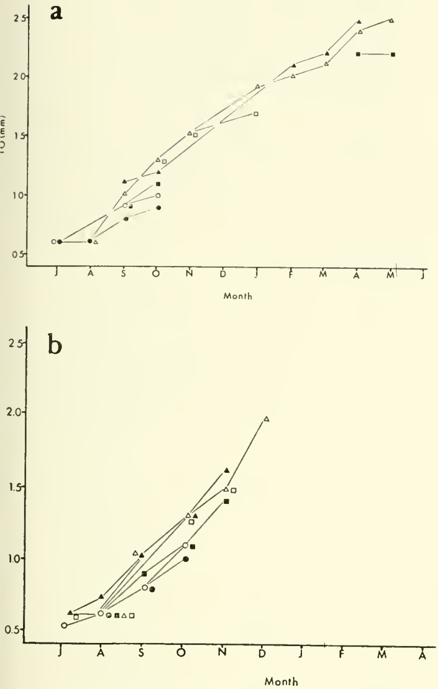

Fig. 4. Comparison of mean cumulative growth of nymphs of (□) *M. signata* at Stations I-V. Station I represented by (o); Station II by (●); Station III by (■); Station IV by (Δ); Station V by (▲); and Station VI by (□): (a) July, 1971 through June, 1972; (b) July, 1972 through December, 1972.

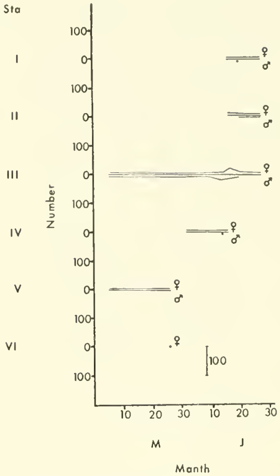

Fig. 5. Emergence at each station of *M. signata*.

tures were 3 C and 5 C, respectively. Emergence ended in late May (water temperature 9 C) at Station V, but lasted until mid-June (12 C) at Station IV and late June (5.5-7 C) at the three upper stations. *Megarcys signata* is a secretive insect that hides in cracks under bridges or among vegetation to escape warm summer temperatures. Clusters of these stoneflies usually containing one female and several males were often collected in these hiding places. Brinck (1949) reported the same phenomenon in related species. The collection data probably reflect this secretive habit in that *M. signata* should have been collected earlier at Station IV.

Females and males generally emerged together in a 1:1 ratio. Harper and Pilon (1970) reported similar findings. Only 55 females and 49 males were collected. Females outnumbered males in both May and June (Fig. 6). There was no size overlap between the females and males. The mean size of females and males decreased as emergence progressed from May to June at all stations (data pooled). Khoo (1968), Schwarz (1970), and Sheldon

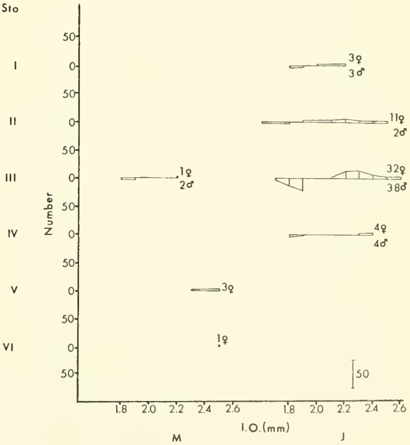

Fig. 6. Frequency distribution of adults of *M. signata*. Number of individuals shown above each polygon.

(1972) reported a similar phenomenon. The mean size of females decreased from 2.4 mm to 2.3 mm, while that of males decreased from 1.9 mm to 1.8 mm (Fig. 7). The data were rather inconclusive because only small numbers of adults were collected in May. More intensive collecting may reveal this trend more strongly. Sheldon (1972) reported similar results in the *Arcynopteryx* species complex he studied and suggested that the decrease in mean size also influenced fecundity; that is, the smaller females carried fewer eggs. Warmer stream temperatures and increasing photoperiod may act as emergence cues before growth and egg development are completed (Khoo 1968, Hynes 1970).

A total of 200 nymphs of *M. signata* were dissected and the foreguts examined for a preliminary food-habit analysis. The nymphs were selected from upper and lower stations and from each season of the year. Table 1 gives the results of this analysis. Of those foreguts examined, 39 were empty (some of these stoneflies were beginning to molt; others had just molted). Chironomids seemed to be the preferred food item. Three types of chironomids based on differences in the head capsules were recognized. Of these three types, one was much more frequently found in the foreguts. A total of 442 were found in 39 percent of the insects examined. The other two types were found only occasionally. Mayflies were the second most abundant food item ingested (37 percent of all individuals). *Baetis* spp. were most frequently recognized. Stoneflies, notably chloroperlids, comprised a considerable portion of the gut contents, also (27 percent of the individuals). Rich-

TABLE 1. Percentage of dissected nymphs of *Megarcys signata* containing specific food items.

Season Date Station No.	Summer 7/20/72 9/8/72 I	Fall 10/15/71 I	Winter 2/4/72 2/18/72 V	Spring 3/17/73 V
Head Capsule Size Range for Sample (mm)	0.4-1.1	0.5-1.4	1.7-2.6	1.9-2.5†
No. Foreguts Examined	25	25	19	31
Empty Foreguts (%)	12	8	26	13
Class Insecta				
Ephemeroptera	5	0	21	63
Plecoptera	9	4	29	49
Trichoptera	4	0	0	3
Diptera				
Chironomidae	32	17	79	26
Other Diptera	0	0	0	0
Unidentified	0	0	7	7
Division Cyanophyta				
Oscillatoria (?) spp.	4;9*	9	0	0
Division Chlorophyta		0	0	0
Mougeotia spp.	0	30;35*	14;21*	0
Enteromorpha spp.	18;14			
Desmids				
Closterium spp.	9	4	0	0
Division Chrysophyta				
Diatoms				
Navicula spp.	100	69;17*	71;21	22
Gomphonema spp.	18	26	29;14*	0
Cymbella spp.	64	39	0	0
Fragilaria spp.	4	22;4*	0	0
Nitzschia spp.	14	43	0	0
Synedra spp.	0	9	0	0
Surirella spp.	23	0	0	0
Diatoma spp.	0	0	0	0
Misc. diatoms	27	48	0	0
Unidentified sp. 1	81;9*	35;65*	43;7*	0
Unidentified sp. 2	50	0	7	0
Unidentified filamentous algae	14	0	0	0
Unidentified plant fragments	0	0	0	0
Detritus (sand grains, silt, plant remains, diatom frustules)	4;77*	4;26*	43;29*	85

†Measurements from 3/17/72
*Dominant

Table 1 (Continued)

Season	Summer	Fall	Winter	Spring	
Date	8/3/72 8/11/71 9/1/71	10/8/71 10/15/71	1/7/72	3/12/73 3/17/73	
Station No.	IV	IV	IV	IV	X
Head Capsule Size Range for Sample (mm)	0.5-1.2	1.0-1.5	1.4-2.3	1.8-2.6†	
No. Foreguts Examined	25	25	25	25	
Empty Foreguts (%)	12	36	36	16	20
Class Insecta					
Ephemeroptera	58	19	75	48	37
Plecoptera	9	19	81	29	27
Trichoptera	0	0	13	0	2
Diptera					
Chironomidae	45	4	88	81	44
Other Diptera	0	0	13	0	1
Unidentified	18	13	4	4	7
Division Cyanophyta					
Oscillatoria (?) spp.	0	38*	0	0	2;5*
Division Chlorophyta					
Mougeotia spp.	23	0	0	0	3
Enteromorpha spp.	0	0	0	0	8;9*
Desmids					
Closterium spp.	4	4	0	0	3
Division Chrysophyta					
Diatoms					
Navicula spp.	0	75*	63*	0	33;22*
Gomphonema spp.	0	50	38	0	20;2*
Cymbella spp.	0	4	0	0	15
Fragilaria spp.	0	0	13	4	6;0.5*
Nitzschia spp.	0	0	0	0	8
Synedra spp.	0	0	0	0	1
Surirella spp.	0	0	0	0	3
Diatoma spp.	0	0	13	0	1
Misc. diatoms	0	0	0	19	12
Unidentified sp. 1	0	19	31	0	25;11*
Unidentified sp. 2	0	0	0	0	7
Unidentified filamentous algae	0	0	0	0	2
Unidentified plant fragments	4	0	0	19	3
Detritus (sand grains, silt, plant remains, diatom frustules)	14	63;4*	0	19	30;17*

†Measurements from 3/17/72
*Dominant

ardson and Gaufin (1971) determined that *M. signata* fed primarily on Ephemeroptera, Chironomidae, and Simuliidae. In his study, Swapp (1972) found that the similar species, *M. subtruncata* (Hanson) and *Skwala parallela* (Frison), ingested mayflies and chironomids and that *S. parallela* ingested caddisflies as well. However, he found only one *S. parallela* of 200 specimens that contained other stoneflies. The food habits of *M. signata* are similar to those of *Skwala curvata* (Hanson) as investigated by Sheldon (1972), with the exception of the number of Trichoptera eaten. In Mill Creek *M. signata* ingested very few caddisflies.

Filamentous algae, diatoms, and detritus also composed a significant percentage of the gut contents. Richardson and Gaufin (1971), Sheldon (1972), and Swapp (1972) report that all the Isogeninae species they studied are herbivores to a considerable extent. Hynes (1941) and Brinck (1949) agree that so-called carnivorous species also feed on vegetable matter. There is no way to determine if these items are actively ingested, present in the prey stomachs, or eaten in the search for prey. The corollary, that the prey species may have been ingested while *M. signata* were grazing on periphyton, may also be true (Sheldon 1972). *Navicula* spp. and an unidentified species of a filamentous diatom were the most numerous of the algae found in the guts. Detritus in the form of sand grains, silt,

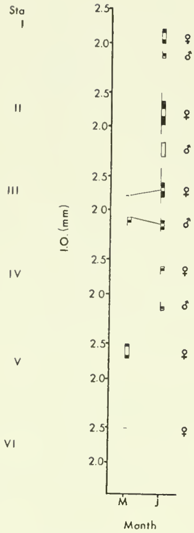

Fig. 7. Size range of adults of *M. signata.*

diatom frustules, leaf fragments, and other plant remains were found in 30 percent of the insects examined. Other diatoms encountered were *Gomphonema* spp., *Cymbella* spp., and *Nitzschia* spp. These are common stream dwellers of Mill Creek, occurring on the rocks in shallow water.

There are some significant seasonal differences in the food items found in the guts. In the summer (July-early September) significantly more *M. signata* (58 percent) ingested mayflies than in the fall at Station IV, but at Station I the numbers feeding on Ephemeroptera were low (5 percent). Stoneflies were found in only 9 percent of the guts examined at Stations I and IV. Chironomids, on the other hand, were present in 32 and 45 percent of the guts at Stations I and IV, respectively. The number of chironomid head capsules found was also greater than in the fall. At Station IV diatoms were notably lacking in the gut contents, although mayflies and chironomids were present. This could be because the swift current dislodges the algae from the substrate and because the deeper water and suspended solids from spring runoff shut out sufficient light. However, at Station I, where the water was shallower, diatoms were found in the majority of the guts examined (*Navicula* spp. were found in all stoneflies examined). Filamentous algae and detritus were also present in many guts. *Enteromorpha* spp., a filamentous green algae, was the dominant plant material in 14 percent of the guts, while detritus was the dominant item in 77 percent of the guts. This herbivorous material may have come from the stomachs of the chironomid prey (mayflies present in only 5 percent of the stoneflies) since Oliver (1971) states that some chironomids feed on algae and detritus. However, many guts contained detritus as the dominant material without chironomids being present. It is conceivable that during the summer the newly hatched nymphs of *M. signata* could feed at least partially on diatoms, filamentous algae, and detritus. At this stage they are probably not as effective a predator as at later life stages. Coffman, Cummins, and Wuycheck (1971) found a similar pattern in other groups of insects, in that young individuals consumed primarily detritus but shifted to algal or animal ingestion as they matured. The lowest absolute growth rate occurs in the summer from July to August despite increased carnivorous feeding. Growth increases sharply from August to September, however.

In the fall (mid-October) at the two stations analyzed, Ephemeroptera were found in 19 percent of the guts at Station IV and in none of the guts at Station I. This can probably be explained on the basis of emergence of many of the mayfly species. One mayfly adult was found ingested, however. Plecoptera were also relatively rare in the fall, many having emerged already. Many summer and fall emergers may still be in the egg stage or too small to be prey. Chironomidae were least numerous at this time of year also (present in only 17 percent of the insects examined). Diatoms and detritus were the most numerous items found in the guts during the fall. Since *M. signata* emerges mostly in the summer, the fall specimens represent some of the smaller sizes. They would not require as much food and thus are adapted to the relative paucity of prey species. At Station IV even diatoms except *Navicula* spp. were not numerous in those stoneflies examined. The swift current could be a factor in removing many from the substrate. At this station more individuals had fed on mayflies and stoneflies than at Station I. Another difference was that more empty foreguts were found in those stoneflies dissected from Station IV (maximum number reached) than at Station I (9 vs. 2). The lack of sufficient prey could be a limiting factor. However, the period October-November represents one of the highest absolute growth rates during the year. The growth rate data were obtained by pooling all samples from all stations, however.

During the winter (January-February) mayflies, stoneflies, caddisflies, and chironomids in the guts increased significantly. Sheldon (1972) reported similar results in some of the *Arcynopteryx* species complex he studied. In the winter at Station IV, there were prey species present in more of the guts than at any other time during the year. This represents an increase in the absolute growth rate but a decrease from the previous month. The calculated absolute growth rates from November to December and from December to January are questionable, since only 3 *M. signata* nymphs were collected in December. This increase in growth rate is probably correlated with the availability of food, because only the family Capniidae are emerging. Chironomids were the most numerous, being present in 88 percent of the guts examined. These slower-moving insects would be easier prey than the faster mayflies and stoneflies. Stoneflies also increased dramatically in the guts despite the fact that the numbers available decreased due to winter emergence. By winter, however, the summer and fall emergers, such as the family Chloroperlidae, may have attained a sufficient size to be suitable prey. Surprisingly, the increase in numbers of prey found in the guts also coincides with one of the periods of the least amount of growth. The low winter-stream temperature could stress the nymphs enough that some growth may be sacrificed even though an adequate food supply may be available. The number of diatoms and other algae decreased significantly, probably due to the decreased water temperature and lack of sufficient solar radiation. Nevertheless, *Navicula* spp. and *Gomphonema* spp. were still numerous. *Enteromorpha* spp. were dominant in 21 percent of the guts examined during this period. The stoneflies dissected from Station V were collected in February, however, when stream temperatures were beginning to warm slightly and solar radiation was increasing. Detritus was present in 43 percent of the guts and comprised the dominant item in 29 percent of those examined. The number of empty foreguts increased to a maximum again during this time.

The early spring (March) was also a time of increased carnivorous feeding. This also coincides with a significant increase in the absolute growth rate. At this time many stoneflies and mayflies are approaching their maximum size prior to emergence. The quiescent stage just before emergence may also make them easier prey. The percentage of mayflies and stoneflies in the guts increased at Station V but decreased at Station IV. One explanation for this may be that during spring runoff, the water level is deeper at Station IV than at Station V. However, the occurrence of chironomids decreased significantly at Station V but remained high at Station IV. The reason for this was not determined. Some emergence could have occurred at Station V, but because the stations are in close proximity this would not seem to be the answer. Sheldon (1972) stated that mature nymphs of the *Arcynopteryx* species complex he studied decrease their consumption of animal food in the spring (April). At this time *M. signata* in Mill Creek undergoes a noticeable decrease in absolute growth rate prior to emergence. Diatoms and other algae were still relatively rare in the guts examined. Presumably spring runoff created spates which might have removed these forms from the substrate. Detritus was found in 85 percent of the guts at Station V. Increased runoff due to snow melt contributed large amounts of allochthonous detritus to the stream. The greater depth of water at Station IV may have prevented the concentration of detritus and effectively removed it. On the other hand, at Station V the channel is wide enough that shallow areas are available for detritus to collect.

In discussing food habits it is important to remember that the partitioning of resources is accomplished by the wide distribution in size range, which decreases intraspecific competition (Hartland-Rowe, 1964; Radford and Hartland-Rowe, 1971). In most samples a difference in interocular measurement of *M. signata* averaged 0.6-1.0 mm from the smallest to largest individuals. This was a significantly larger size range than in the euholognathan species studied.

Acknowledgments

This study is part of a Ph.D. research project by the senior author. The authors wish to thank Bill P. Stark for his helpful suggestions.

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RECORDS OF STONEFLIES (PLECOPTERA) FROM NEVADA[1]

Mary R. Cather,[2] Bill P. Stark,[2] and Arden R. Gaufin[2]

Abstract.— Distributional data are presented for 13 species of Nevada stoneflies including eight species new to the state list. A checklist of 30 species confirmed for Nevada is included.

The Nevada stonefly fauna has received scant attention from collectors working the intermountain region. A review of the literature reveals 22 species recorded from the state, most of these without specific distributional data.

We are reporting eight additional species, *Pteronarcys princeps* Banks, *Isoperla fulva* Claassen, *Isoperla patricia* Frison, *Hesperoperla pacifica* (Banks), *Utaperla sopladora* Ricker, *Alloperla severa* Hagen, *Sweltsa coloradensis* (Banks) and *Malenka tina* (Ricker). Distributional data are presented for these species as well as new records for species previously reported.

We thank R. W. Baumann, U. S. National Museum, for species records.

Pteronarcella badia (Hagen).—New Records: *Humboldt Co.*, Cottonwood Creek near Paradise Valley, 30-VII-68, nymphs.

Pteronarcys californica Newport.—New Records: *Washoe Co.*, Reno, 18-VII-51, T. H. Zehrbach, 1 ♂.

Pteronarcys princeps Banks.—Distribution: *Elko Co.*, Franklin River, Highway 11, 19-IX-57, G. F. Edmunds, Jr., and R. K. Allen, nymph; *Lander Co.*, Big Creek, 9-IX-54, T. C. Frantz, nymphs; Big Creek, Big Creek Campground, 14-VI-74, B. P. Stark, 18 ♂ 11 ♀, nymphs.

Skwala parallela (Frison).—New records: *Elko Co.*, Columbia Creek, 20-IX-57, G. F. Edmunds, Jr. and R. K. Allen, nymphs; Secret Creek at Secret Pass, 15-VI-74, B. P. Stark, exuvium; same location, 4-VII-74, M. and E. Cather, nymph; *Washoe Co.*, Reno, 9-III-41.

Isoperla fulva Claassen.—Distribution: *Elko Co.*, Secret Creek, Highway 11, 15-VI-74, B. P. Stark, ♂♂ ♀♀; Secret Creek, Secret Pass, 15-VI-74, B. P. Stark, ♂♂ ♀♀.

Isoperla patricia Frison.—Distribution: *Humboldt Co.*, 5 miles north of Paradise Valley, 18-VI-67.

Doroneuria baumanni Stark and Gaufin.—New Records: *Lander Co.*, Big Creek, Big Creek Campground, 14-VI-74, B. P. Stark, nymphs; *Nye Co.*, South Twin River, 10-VII-54, T. C. Frantz, nymphs; Ophir Creek, 4-X-54, T. C. Frantz, nymphs.

Hesperoperla pacifica (Banks).—Distribution: *Elko Co.*, Willow Creek, 10-I-65, C. Murvosh, nymph; Secret Creek, Highway 11, 15-VI-74, B. P. Stark, 2 ♀; Secret Creek, Secret Pass, 15-VI-74, B. P. Stark, 1 ♂ 1 ♀; Lamoille Creek, 2 miles above Camp Lamoille, 6-VII-74, M. and E. Cather, 1 ♂, nymphs.

Utaperla sopladora Ricker.—Distribution: *Elko Co.*, Lamoille Creek, 2 miles above Camp Lamoille, 6-VII-74, M. and E. Cather, mature ♂ nymph.

Alloperla severa Hagen.—Distribution: *Elko Co.*, Secret Creek, Highway 11, 15-VI-74, B. P. Stark, 11 ♂ 10 ♀; Secret Creek, Secret Pass, 15-VI-74, B. P. Stark, 1 ♂ 2 ♀.

Sweltsa coloradensis (Banks).—Distribution: *Elko Co.*, Secret Creek, Secret Pass, 15-VI-74, B. P. Stark, 1 ♂; Lamoille Creek, 2 miles above Camp Lamoille, 6-VII-74, M. and E. Cather, 2 ♂ 1 ♀, nymph; *Lander Co.*, Big Creek, Big Creek Campground, 14-VI-74, B. P. Stark, 13 ♂ 9 ♀; *White Pine Co.*, Lehman Cave, Baker, 11-VI-61, S. G. Jewett, Jr., 6 ♂ 3 ♀.

Triznaka pintada (Ricker).—New records: *Clark Co.*, Deer Creek, 5-VIII-69.

Malenka tina (Ricker).—Distribution: *Elko Co.*, Secret Creek, Secret Pass, 15-VI-74, B. P. Stark, 1 ♂ 2 ♀.

Nevada List

The following is a checklist of the 30 species confirmed as occurring in Nevada.

Pteronarcidae

Pteronarcella badia (Hagen)
P. regularis (Hagen)

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[1] Study supported by NSF Grant No. 6986-609 and EPA Grant No. 3053-364.

[2] Department of Biology, University of Utah, Salt Lake City, Utah 84112.

Pteronarcys californica Newport
P. princeps Banks

Peltoperlidae

Sierraperla cora (Needham and Smith)
Soliperla thyra (Needham and Smith)

Perlodidae

Kogotus modestus (Banks)
Skwala parallela (Frison)
Isoperla fulva Claassen
I. marmorata Needham and Claassen
I. patricia Frison

Perlidae

Doroneuria baumanni Stark and Gaufin
Hesperoperla pacifica (Banks)

Chloroperlidae

Utaperla sopladora Ricker
Alloperla severa Hagen
Suwallia pallidula (Banks)
Sweltsa coloradensis (Banks)
S. pacifica (Banks)
Triznaka pintada (Ricker)
Chloroperla cydippe Newman

Needham and Claassen (1925) recorded this species from Washoe Co., Reno. We have not examined the specimens but they probably are *Hastaperla chilnualna* Ricker.

Nemouridae

Malenka californica (Claassen)
M. coloradensis (Banks)
M. tina (Ricker)
Podmosta delicatula (Claassen)
Prostoia besametsa (Ricker)
Soyedina nevadensis (Claassen)
Zapada cinctipes (Banks)

Capniidae

Capnia lacustra Jewett
Utacapnia tahoensis (Nebeker and Gaufin)

Leuctridae

Paraleuctra occidentalis (Banks)

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GROWTH OF PLECOPTERA (STONEFLY) NYMPHS AT CONSTANT, ABNORMALLY HIGH TEMPERATURES[1]

Joseph M. Branham[2], Arden R. Gaufin[2], and Robbin L. Traver[2]

Abstract.— Six species of Plecoptera were maintained at four different temperatures, which were constant and higher than occurred in the natural habitat, and three species at two different day lengths. Each animal was weighed each day or each week. Weight of two species in the wild was monitored from periodic collection.

The weight of each animal fluctuated rhythmically, changing about five percent every five days. These short-term fluctuations probably resulted from changes in water content. Molting occurred when a peak weight was predicted from the cycle and involved temporary gain of about 20 percent in weight. Growth probably stopped for some time before molt and was most rapid just afterward. Many animals died at molt.

The time before death was less for univoltine species than for those with longer life cycles. Plecoptera collected in winter from water near 0 C lived for shorter times than did those collected in autumn from water near 10 C. Two species died sooner at higher temperatures and one died sooner with shorter day lengths.

Growth in the laboratory was generally slower than in nature. One species grew faster, while three grew more slowly at higher temperatures. One species grew faster under long- than short-day conditions.

Premature emergence, expected at the higher temperatures, did not occur, except in one animal.

Calefaction, or abnormal warming, can alter the life span of some aquatic insects. Some die soon after being experimentally exposed to higher than normal temperatures. Others acclimatize and may emerge prematurely (Nebeker and Lemke, 1968; Nebeker, 1971). Effects of constant, higher-than-normal temperatures on the growth and development of aquatic insects are, however, little understood.

Temperature changes could be important cues to growth and seasonal emergence. Species living in or near springs, where the temperature is relatively constant and does not become as cold as in neighboring streams, frequently emerge unseasonably (Thorup, 1963). Alternately, temperature changes are necessary for normal development of some insects (Hodson and Rawy, 1956). Such changes lead to considerable biochemical restructuring on a seasonal basis (Somero and Hochachka, 1971) and can also affect gene expression and the phenotype of insects (Sanderson, 1910; Wigglesworth, 1965; Waddington, 1957). The elimination of temperature changes could, therefore, interfere with normal development.

Abnormally high temperatures could have long-term cumulative effects on growth and development (Sander, 1910; Richards, 1956, 1957). Growth could be faster than normal because chemical rates generally accelerate, or slower because metabolic equilibria are upset (Ludwig, 1910). The effect on growth could in turn influence development, emergence, and adult function.

Understanding the effects of temperature on growth and development of aquatic insects would be useful in appraising the effects of thermal pollution, because larval insects are an important component of aquatic environments, particularly streams (Hynes, 1970). The purpose of this research was to elucidate the growth patterns of some species of Plecoptera maintained in the laboratory at different temperatures. Stonefly nymphs were chosen because they develop in winter and spring when the stream temperatures are often near freezing and because they are abundant. Three carnivorous and three herbivorous species were collected in autumn 1972 and established in the laboratory at four different temperatures and two different day lengths. Some were examined and weighed daily; others, weekly. Growth patterns of individuals were plotted, and statistical comparisons were made between groups of animals under different conditions.

Materials and Methods

Some features of the species studied are outlined in Table 1. All were collected in October, when stream temperatures

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[1] This investigation was supported by Research Contract No. 14-12-438 from the National Water Quality Laboratory, Federal Water Pollution Control Administration, to the University of Montana Biological Station, Bigfork, Montana.

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TABLE 1. Collection sites and activity cycles of species studied.

	Family	Time of Normal Emergence†	Years in Life Span	Collection Sites
Nemoura cinctipes	Nemouridae	Jan.-May	1	Mill Creek, Salt Lake Co.
Pteronarcella badia	Pteronarcidae	May-Sept.	1	Upper Provo R., Wasatch Co.
Pteronarcys californica	Pteronarcidae	Apr.-Aug.	>1	Lower Provo R., Utah Co.
Arcynopteryx signata	Perlodidae	June-July	1	Mill Creek, Salt Lake Co.
Acroneuria pacifica	Perlidae	Mar.-Sept.	>1	S. Fork Provo R., Utah Co.
Claassenia sabulosa	Perlidae	June-Aug.	?	Weber R., Summit Co.

†Gaufin, Nebeker, and Sessions, 1966

were 10-12 C, and the experimental groups were established in the first part of November, except where noted below.

The specimens were maintained separately in perforated plastic (polyethylene) drinking cups 9.5 cm in depth and 7 cm in top diameter, tapering to 5 cm at the bottom. The cups were suspended and were about half submerged in stainless steel aquaria approximately 100 cm long, 17 cm wide, and 15 cm deep and having a 25.5 L^3 volume. Nine such aquaria were suspended in two refrigerated water baths; four in a bath at 9.5 C and five in another bath at 13 C. Each aquarium was heated with a thermostatically regulated element. Tap water flowed through each aquarium at about 0.4 L/min. (or about one aquarium volume/hour). Each aquarium was aerated with filtered compressed air and agitated with a paddle wheel that mixed the water in the aquarium and caused a predominantly up-and-down oscillation of water in the cups. Concentration of dissolved oxygen remained greater than 90 percent of saturation in the cups. Temperature was maintained with a standard error of ± 0.02 C and a range of about ± 0.5 C, at 10, 12, 14, or 16 C. These aquaria were lighted from about one meter above with two fluorescent bulbs on a 12-hr. light, 12-hr. dark cycle. Ambient room light, which was not excluded, varied somewhat.

In a separate experiment to estimate the effect of light periodicity, three species were maintained in cups suspended in plastic aquaria flushed with aerated running water (1 vol./hr.) but with no paddle wheel (dissolved O_2, $>$ 90 percent saturation). These were in a walk-in cold room that maintained the water temperature at 11.5 C within the same limits as in the other aquaria. They were illuminated with fluorescent lights (2 bulbs) that delivered about 400 Lux at the water surface on either a 12L, 12D (long-day) or a 6L, 18D (short-day) periodicity (Beck, 1968).

One or several small stones and several decaying leaves (cottonwood, *Populus angustifolia;* or maple, *Acer grandidentatum*) were kept in each cup. Herbivorous species were also supplied a few pellets of Purina® rabbit chow every few days, and the carnivorous ones were kept supplied with a mixture of small aquatic organisms, including amphipods, chironomids, ephemeroptera, oligochaetes, and flatworms collected from near a local fish hatchery.

Changes in weight were monitored either each day between 1 and 3 PM or each week on Thursday between 1 and 5 PM. Each animal was gently blotted with a Kimwipe® (Kimberly-Clark Cororoporation), air-dried for half a minute, and weighed to the nearest 0.1 mg on a Mettler H6T balance. The standard error of the method, determined by repeatedly weighing the same animals about 20 times in an hour, was about 0.002 of the mean for animals about 200 mg, about 0.005 of the mean for ones about 150 mg, and about 0.01 of the mean for animals about 30 mg. Repeated weighing revealed a gradual but statistically significant decrease in weight of each animal even though they were returned to the water between each determination, so the standard error of single weighings each day or week may have been less than for about 20 weighings an hour.

Natural growth rates were calculated for *Pteronarcella badia* and *Arcynopteryx signata* from approximately monthly collections of 22 specimens of each species from the initial site. The animals were weighed as above, within several hours of collection, and growth was determined as the rate of change of the average weight.

The data were evaluated by regression

analysis (Rao, 1958; Bailey, 1959; Alder and Roessler, 1968), using a Hewlett Packard 9100 B computer and programmed procedures supplied by the manufacturer. Growth trends of each individual were analyzed from weight data by determining the correlation coefficient (r) and, from it, the possibility that changes in weight were correlated linearly with time, according to the calculated slope (m) which intercepted the axis representing weight at the hypothetical initial weight (b) independent of fluctuations at the beginning of the observations. Growth was judged to be positive, negative, or insignificant from the correlation coefficient ($P > .05$), and its magnitude was determined from the slope. Absolute growth values, in weight units, were converted to relative ones for comparisons between animals by determining the rate of change as a percentage of the averaged initial weight ($m \times 100/b$). The effects of various conditions were then evaluated by t-test or regression analysis, using the relative growth rates.

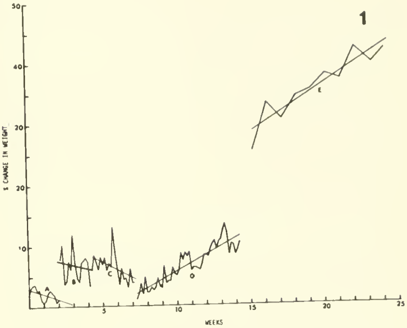

Fig. 1. Weight changes of a *Pteronarcys ca fornica* kept under various conditions. This ind vidual was collected in December and acclimatiz d to laboratory conditions for 15 days without foo It was then weighed daily while being starved A 14 days), fed rabbit chow B (15 days), and the leaves and rabbit chow C (21 days), while being ept at 10 C. It was then changed to 16 C an weighed daily while being fed leaves and rabbit how D (50 days) and finally weighed once eac week for 10 weeks (E). It did not molt and w s still alive after the 170-day observation period.

SHORT-TERM FLUCTUATIONS IN WEIGHT

The weight of all stoneflies examined every day increased and decreased rhythmically, typically varying 3 to 25 percent of the body weight about every 4-6 days (Table 2; Figs. 1, 2, and 3). The magnitude of weight difference between high and low periods exceeded the probable error due to the method, and the trends apparent in the plotted data indicate that the fluctuations were not merely artifacts of the method. There was no apparent correlation between the rhythmic pattern and environmental conditions, nor were the cycles of different animals in phase with each other, even though they were in the same aquarium.

It was hypothesized that periodic feeding behavior caused the observed rhythmic weight changes. To test this, ten *Pteronarcys californica* (collected 5 De-

TABLE 2. Periodic variations seen with daily weighings (Average ± SE) calculated from the first six cycles.

	No. of animals	Period (days between peaks)	Amplitude*
P. californica	5	5.9 ± .4	3.3 ± .3
P. badia	4	4.5 ±1.0**	5.4 ±1.6
A. pacifica	5	5.0 ± .4	7.2 ±1.0***
C. sabulosa	1	4.7	5.7
A. signata	1	6.3	12.3

*Difference between peaks and troughs, expressed as percentage of average weight.
**Significantly ($p < .05$) different only from *P. californica*
***Significantly ($p < .001$) different only from *P. californica*

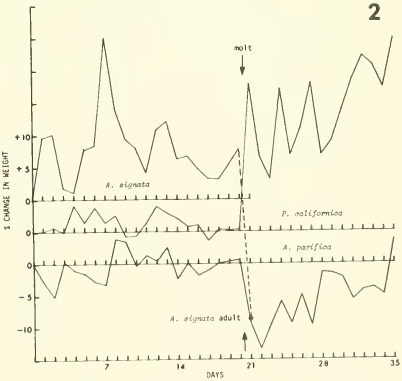

Fig. 2. Daily weight changes before and a er molting (*Pteronarcys californica* and *Acroneur* *pacifica*) and before emergence (*Arcynopteryx si* *nata*). The molted cuticle was found and the an mal weighed about six hours after the molt occu ed.

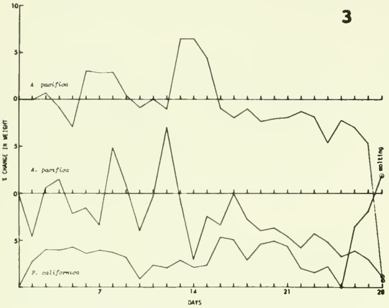

Fig. 3. Daily weight changes before death.

cember 1972) were starved for 15 days without weighing; then weighed every day for 14 days, while starving; then fed either Purina rabbit chow or decaying leaves and weighed daily for 15 days; and, finally, fed the other food and weighed daily. Starvation did not eliminate the rhythmic weight changes (Fig. 1), although all the animals were losing weight. The periodicity remained unchanged upon feeding either or both foods. The amplitude was not affected significantly (P > .05) when leaves were supplied but was significantly increased over the starvation level after feeding rabbit chow, either alone or with leaves (Table 3).

The rhythmic weight changes could have been associated with molting. Weight changes during molting were observed in a few specimens. Of the 16 animals weighed daily, five molted one time successfully, one emerged, and six died molting. One *Ps. californica* and one *Acroneuria pacifica* were weighed during a successful molt. The *Ps. californica* was 24.4 percent heavier at the time of molting than just before, and the *A. pacifica* was 19.0 percent heavier. The ones that died molting were all considerably heavier than they had been (Table 8). Molting generally occurred when the pattern of weight change indicated that a peak weight was due to occur. After molting, the period between weight maxima was usually shorter and the amplitude greater than it had been before the molt; but after several cycles, the pattern began to resemble the premolt condition again.

The one animal on a daily weighing schedule that emerged (an *Ar. signata*, Fig. 2) also molted and emerged at a peak in the weight cycle. The adult was 25 percent lighter than the nymph. Its gut was empty.

The frequency of weighing affected the weight of stoneflies. Animals weighed a number of times in an hour lost weight during the course of the observations. Five animals that had been weighed every day gained weight appreciably when the weighing frequency was reduced to once a week. The growth rate (m) was usually slightly greater with the less frequent weighings, but the change in rate was not statistically significant (Fig. 1). Handling could have caused the animals to contract and expel water or gut contents, and it likely interfered with feeding patterns.

Long-term Growth Patterns

The stoneflies under observation lived for various periods. Those that lived a month or more either gained, lost, or remained the same weight during their

Table 3. Effects of food on periodic variation, seen with daily weighings of *P. californica* (average ± SE).

	N	Period (days between peaks)†	Amplitude (difference between peaks & troughs, expressed as a % of average wt.)	Gain after feeding (% of previous wt.)
Starved	10	5.1 ± 1.0	2.2 ± .3	
Fed leaves	3††	5.6 ± 1.0	3.1 ± .3	4.3 ± .3
Fed rabbit chow	4††	5.3 ± 1.2	5.3 ± .4**	11.8 ± .6
Fed both	7††	5.1 ± 1.2	4.4 ± .5*	8.7 ± .5‡

†Estimated from three peaks

††Three that did not respond to either food were excluded from these calculations

‡Only those fed rabbit chow after leaves responded

*Significantly different (p > .01) from starved group only

**Significantly different (p > .001) from starved group only

TABLE 4. Average (X ± SE (N)) Weeks of life.

	10 C	12 C	14 C	16 C	Long Day (11.5 C)	Short Day (11.5 C)
P. californica†	25.2±3.0(5)	17.2±2.1(6)	24.5±4.9(6)	23.8±4.6(6)		
P. badia	15.0±2.5(5)	17.7±1.3(6)	11.4±2.1(6)	10.7±1.6(6)	6.0±1.1(11)	6.7± .6(11)
N. cinctipes	4.7± .9(6)	6.2±1.2(6)	2.5± .3(6)	4.7± .9(6)		
A. pacifica	18.9±5.8(5)	16.5±3.5(4)	18.0±4.3(6)	14.2±4.3(5)	15.6±1.9(11)	11.1±2.6(11)
C. sabulosa	17.0± .1(2)	17.5±1.5(2)		9.7±1.1(3)		
A. signata	9.5±3.1(4)	9.3±1.7(4)	2.7± .6(7)	2.8± .4(12)	3.4± .9(7)	2.7± .6(7)

†Eight *Ps. californica* and three *Ac. pacifica* were still alive at the time of writing, 35 weeks after the observations began.

life. Some individuals lost weight for part of their life and gained in another part. It was important to consider the history, length of life, and ultimate fate as well as the overall growth patterns in assessing the effects of temperature on growth rate.

Some species lived longer in the laboratory than did others (Table 4). In general the smaller, univoltine species, *Nemoura cinctipes*, *Pa. badia*, and *Ar. signata*, did not live as long as the larger species, *Ac. pacifica*, *Claassenia sabulosa*, and *Ps. californica*, which probably live for several years as nymphs (Table 1). *Pteronarcella badia* and *Ar. signata* lived for significantly ($P > .05$) less time at higher temperatures. *Pteronarcella badia*, *Ar. signata*, and *Ac. pacifica* kept in the light-control chambers died significantly sooner than their counterparts in the temperature experiments. The former were caught in winter from streams near 0 C and were kept without stirring. Day length had no significant effect on the life span of *Ar. signata* and *Pa. badia*.

Weight changes prior to death followed three distinctive patterns, which, in some specimens, could have been related to cause of death (Fig. 3, Table 5). Often death occurred during a recognizable molt. Sometimes the growth curve turned sharply up, as if molting, but there was no external sign of molting. More often, death followed a diminuation in the amplitude of cyclical weight changes and was not marked by any sharp change in weight. Two *Ps. californica* that did not change in weight upon being supplied with either food showed this pattern, and it may have reflected starvation. The third pattern was marked by a sharp loss of weight at death. Adults weighed less after emerging (Fig. 2), and such sharp terminal weight loss could have indicated unsuccessful emergence. The circumstances of death of all animals that died are presented in Table 5.

Periodic molting is a characteristic of Arthropod growth. However, many of the animals observed here apparently did not molt, while many others died in the process (Table 5). No *N. cinctipes* and only one *Ar. signata* were observed to molt. The occurrence and frequency of molting for the other species are enumerated in Table 6. Some molts were probably overlooked, but the analysis of growth curves suggests that most were detected by the presence of the cast cuticle.

The times until first molt, between molts, and until death for ones that did not molt are compared in Table 6. Time before the first molt (considering ones that molted successfully or that died molting) was quite variable and was probably a function of the condition of the animals at the time of capture. The time between molts was also highly variable. The average period before the first molt was not significantly different from the time between molts for any species. The average length of life of individuals that did not molt was also the same as the average period before the first molt and the period between molts. The average period before molt differed between species: *Ps. californica* = *C. sabulosa* > *Ac. pacifica* > *Pa. badia* (t-test, differences considered significant if $p > .05$). There was no cor-

TABLE 5. Circumstances of death (percentage of N).

	N	M†	1†	2†	3†	E†
P. californica	31††	8	26	50	15	0
P. badia	52	21	20	53	3	2
N. cinctipes	22	0	0	100	0	0
A. pacifica	40††	26	11	52	10	0
C. sabulosa	8	57	0	28	14	0
A. signata	42	2	11	74	11	2

†1 Growth curve turned up at death, as prior to molting
2 Growth curve continued unchanged until death
3 Growth curve turned down at death, as prior to emergence
M Died molting
E Emerged

††Four additional *P. californica* and two *A. pacifica* were accidentally killed.

TABLE 6. Occurrence and frequency of molts

	Number observed† molting				Weeks (average ± SE (range))		
	0x	1x	2x	3x	Before first molt	Between molts	Of life of ones not molting
P. californica	28	3	3	0	16 ± 3 (12-30)	15 ± 3 (10-19)	17 ± 2 (3-32)
P. badia	30	16	4	2	5 ± 1 (1-18)	7 ± 1 (1-11)	5 ± 1 (1-19)
A. pacifica	15	17	10	0	9 ± 1 (2-21)	9 ± 1 (2-18)	8 ± 1 (3-22)
C. sabulosa	1	7	0	0	15 ± 1 (13-17)		6 ± 3 (3- 8)

†Molting recognized by finding a cast cuticle or found dead in the process of molting.

relation between size and the length of time before or between molts either within or between species. There was also no correlation between the length of time before molts and the temperature or light period for any species examined.

Changes in weight accompanied molting (Table 7). Most animals weighed during a molt (alive or dead) showed a dramatic increase over the premolt weight. Usually this increase was much greater than the longer-term increase (determined by comparing the average weight the month before molt with the average weight for the month afterward) and could have been associated with the mechanism of molting. Animals that molted several times, and thus apparently were adapted to laboratory conditions, grew appreciably between molts. Some of the ones that died without molting grew about the same amounts as did others between molts, suggesting that death could have resulted from failure to molt.

For each animal observed, the growth rate (calculated as the regression coefficient [m]), for the four weeks prior to molting usually was different from that for the month after molt (Table 8). There was a great deal of variability between individuals: some lost before and gained after; some gained before and lost after; some gained or lost more rapidly before than after; and vice versa. One *Ps. californica* lost 1.0 percent/week for 20 weeks, molted, and then gained 1.1 percent/week for 15 weeks. The growth patterns in Fig. 2 are from apparently normal animals that lived many months in the laboratory. The number that molted and lived at least a month afterward was small, so averages and limits (Table 8) do not indicate significant (p > .05) differences in average pre- and postmolt rates. There was no significant correlation with the controlled parameters of temperature or light.

The overall growth of each animal until death was evaluated by calculating the correlation coefficient (r) and the regres-

TABLE 7. Change in weights with molting.

	Percent change in weight (average ± SE (range)).							
	N	During molt†	N	With molt††	N	Between molts‡	N	Total, ones not molting‡‡
P. californica	4	26± 2(22-30)	6	25±5(9-41)	3	22.6±4.9(13.1-29.1)	28	19.4±10.1(-22.8-174.3)
P. badia	10	65± 6(36-85)	10	12±4(5-32)	5	9.8±5.7(-1.2-20.4)	30	21.6± 6.9(-25.1-144.4)
A. pacifica	12	22± 4(3-47)	12	2±2(-9-19)	8	15.6±5.5(0.7-48.6)	15	-3.8± 1.6(-14.4- 9.2)
C. sabulosa	4	36±14(18-78)	3	1±7(-8-15)	0		1	10.0

†Animals weighed during a successful molt or found dead in the process of molting. Weight during molt as a percentage of the last premolt weight.
††Average weight for the month after molt as a percentage of the average for the month preceding the molt.
‡Calculated from the growth curve. Slope multiplied by the time and expressed as a percentage of the intercept (i.e., the hypothetical initial weight).
‡‡Total growth calculated as m x weeks of life x 100/b.

TABLE 8. Growth rates (percentage change/week) before and after molt (m ± SE (range)).

		Month before molt	Month after molt
P. californica	6	-.16 ± .84 (-3.35 - 2.05)	2.79 ± .81 (.09 - 5.75)
P. badia	9	2.73 ± 1.34 (-2.37 - 10.69)	-.39 ± 1.29 (-9.76 - 5.75)
A. pacifica			
All	26	.54 ± .41 (-2.68 - 6.32)	1.17 ± .56 (-3.23 - 10.98)
Long day	7	.96 ± .99 (-3.68 - 3.46)	3.23 ± 1.20 (- .05 - 10.96)
Short day	5	-.02 ± .50 (-2.53 - 1.69)	-.30 ± 1.00 (-3.23 - 1.69)
C. sabulosa	3	.38 ± 2.07 (-2.71 - 4.33)	-2.04 ± .78 (-3.57 - -1.08)

sion coefficient (m) in 0.1 mg change/week. The overall growth rate was sometimes influenced strongly by the final phase of the growth curve as the animal expired. Growth during the first two months was therefore calculated separately. To simplify comparison between species and experimental groups (Table 4) the growth rate (m) was expressed as a percentage of the calculated initial weight (b, the intercept). The number of animals was so small and the range of values so great within each group that averages and standard errors are of little meaning. Regression analysis of rates of change against temperature, however, indicated that temperature had a significant effect on the growth rates of some animals (r significant at $p > .05$). The proportionate (percentage) effect of temperature on growth rate, exclusive of experimental error, is expressed as the coefficient of determination (r^2 x 100) (Alder and Roessler, 1968). The relationship between difference in growth rate per degree Celsius is expressed by m.

These observations were apparently valid only for the animals collected in October and November, when the stream temperatures were still about 10 C. The few animals collected later in the year from colder streams died in a shorter time and generally grew at rates different enough from the others' that it seemed best to exclude them from the preceding calculations.

Light periodicity could also have affected development in the laboratory. Significantly more *Pa. badia* molted under long- than short-day conditions. There was no significant difference in length of life or growth rate between animals of either species held under long- or short-day conditions. *Acroneuria pacifica* lived longer under long-day conditions (15.5 ± 2.0 vs 10.2 ± 2.3 weeks) but molted sooner under short days (7.1 ± 1.5 vs 9.1 ± 1.5 weeks). Significantly more molted under long than short days. Their growth rate to death was significantly greater under long days (1.9 ± .8 percent/week) than under short days (-1.0 ± .3 percent/week) (Table 6). These animals were not strictly comparable to the ones used for the temperature experiments: the water in their tanks was not stirred, and they were collected later in the year (*Pa. badia* and *Ac. pacifica* in November and *Ar. signata* in February). *Pteronarcella badia* and *Ar. signata* kept under equal periods of light and dark died significantly sooner than ones under similar light and temperature conditions but collected earlier and kept in stirred water (Table 4).

Laboratory conditions were quite different from nature, so it was desirable to compare growth of laboratory and wild animals from natural populations where possible. *Pa. badia* and *Ar. signata* persisted at the initial collecting sites in populations of relatively uniform-sized individuals. Their growth in nature was quite linear for both species between October and May 9 (Fig. 4). The average percentage of weight increase per week of wild *Pa. badia* was 6.26 ± 0.5 ($r = .998$), and that of *Ar. signata* was 10.17 ± .07 ($r = .938$). Such an analysis was impractical with the larger species because of the simultaneous existence of several year classes and the effect of investigator selection. Wild *Ar. signata* emerged naturally in May (water temperature 5-8 C) and *Ps. californica*, *Pa. badia*, and *Ac. pacifica* in May (water temperature 10-11 C).

Discussion

Stonefly naiads varied in weight as time passed. Some of the variation was associa-

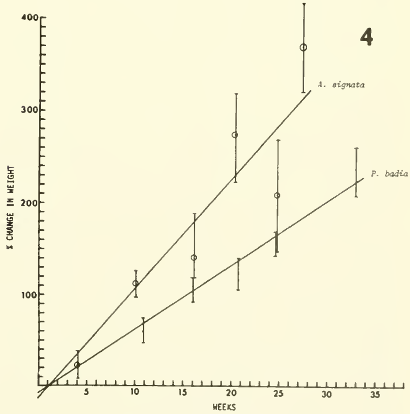

Fig. 4. Growth of *Pteronarcella badia* and . *rcynopteryx signata* in the stream. Means (wit SE) were calculated from periodic samples of 22 nimals and converted to percentage of the averag initial weight.

ted with short-term fluctuation in state, while some represented long-term "growth." Variation in gut content rapidly altered the weight of experimental animals as much as 10 percent or more (Fig. 1, Table 3). Cyclical weight changes, on the order of 5 percent variation every 5 days (Tables 2 and 3), occurred even in the absence of feeding and could have resulted from the amount of water in the animal, in either its gut or its tissue. This cyclical weight change could have been associated with molting. Each animal that was observed daily and that molted did so when a predicted peak weight should have occurred, and animals weighed considerably more when molting than just before or after the molt (Table 7). Such rapid weight gain could be responsible for splitting the old cuticle and filling out the new one (Wigglesworth, 1965).

The failure of molting was a common cause of death of animals in the laboratory. Many animals died during or just after molting. Others died at a time of peak weight, considerably above the previous average, as if about to molt (Fig. 3, Table 5). Most of the animals died without any molts except for *Ac. pacifica* and *C. sabulosa* (Table 6). On the average, those that did not molt died approximately when they should have molted, as judged from the average time before or between molts. Their average growth was also about the same as the average growth between molts of animals that survived in some species (Table 7). No *N. cinctipes* and only one *Ar. signata* were observed to molt, and their average life was less than for the other species (Table 4). It seems likely that failure of some aspect of molting was a common cause of death of stoneflies kept in the laboratory.

Relatively few animals lived long enough with repeated molts (Table 4) to be considered normal. The one *P. badia* that emerged (kept at 16 C) molted the first week in the laboratory (1 Nov.) with a 19 percent gain in weight, gained 28 percent more in the next 8 weeks, and emerged in January, 5 months prematurely. Its growth was almost linear from the beginning of the observations ($r = .998$) and slightly less ($m = 5.2$ percent/week) than the average for the species in nature. Most of the *P. badia* that molted successfully and then lived for at least a month gained weight prior to, and as a result of, the molt, but then lost weight (Tables 6, 7). Food may have been deficient, or the newly molted ones may have been less tolerant of laboratory conditions. Two *P. californica* that lived for the entire 35-week observation period molted twice each. Both lost weight the month before the first molt and showed no significant change the month before the second molt. Both gained considerable weight at both molts, remained at a higher weight, and continued to grow at an accelerated rate after the molt (Fig. 2, Tables 6, 7, and 8). They apparently did not feed before the molt, expanded in volume during the molt, and, at the larger volume, hardened and began to eat. The four *Ac. pacifica* that lived for the duration of the observations usually were not growing significantly prior to molt, expanded appreciably during the molt, but then declined to a weight considerably below the premolt weight within a day or so. They then grew rapidly for several weeks, until the previous weight was reached, after which they did not grow significantly again until after another molt. Some regressed at molting and lost weight overall (Table 7) (Fig. 2, Table 9). Probably their pattern was not normal but reflected subsistence in an unnatural environment (Beck and Bharadwaj, 1972).

The anticipated premature emergence (Nebeker, 1971) was not found. Of the animals collected in October, only one (*Pa. badia*) emerged and only a few died with a pattern of weight changes even suggesting emergence (Table 4). This could have been because the animals were collected early in the autumn and kept at constant temperatures and long-daylight conditions at or above those existing at the time of collection. Perhaps some environmental cue was absent. Or possibly the small plastic cups in which the animals were kept were too confining to permit normal behavior. A number of *P. californica* collected from streams near O C in January, acclimatized to 16 C, and kept communally in fish-breeding nets in the laboratory did emerge in March, three months before the wild population emerged naturally. One *Ar. signata*, collected in February, emerged 22 days after being put in a cup and kept at 10 C (Fig. 2).

The length of life of *Pa. badia* and *Ar.*

TABLE 9. Growth rates (m = percentage change in weight/week) and temperature, all data to death (upper half), and first two months only (lower half).

		10 C		12 C		14 C		16 C		Regression, growth rates against temperatures			
		N	$\bar{m}$† ± SE	N	$\bar{m}$† ± SE	N	$\bar{m}$† ± SE	N	$\bar{m}$† ± SE	N	m††	r	%r²
P. californica	all	5	.60 ± .23	6	.02 ± .48	6	1.00 ± .85	5	1.60 ± .86	22	0.25	.346	12
	+	3	.66 ± .25	2	1.23 ± .88	4	2.13 ± .65	5	1.60 ± .86				
	—	1	-.45	3	-.83 ± .25	1	-2.30	0					
P. badia	all	5	5.14 ± 1.53	6	2.79 ± .66	6	3.84 ± .68	7	1.53 ± 1.04	24	-0.49	-.417*	17
	+	4	3.58 ± .66	6	2.79 ± .66	6	3.84 ± .68	4	3.18 ± 1.07				
	—	0		0		0		1	-2.79				
N. cinctipes	all	6	2.14 ± 2.47	4	3.11 ± 3.60	3	-5.54 ± 4.97	5	-.88 ± 1.45	18	-0.77	-.290	8
	+	1	2.77	1	13.87	0		0					
	—	0		1	-1.32	1	-1.65	1	-2.21				
A. signata	all	4	2.63 ± 1.68	4	.50 ± 1.20	4	-.53 ± 1.34	12	-1.41 ± 1.72	24	-0.39	-.380	14
	+	0		1	3.93	0		1	1.63				
	—	0		0		0		0					
A. pacifica	all	5	.63 ± .48	4	.25 ± .45	6	.13 ± .42	5	.00 ± .59	20	-0.10	-.223	5
	+	3	1.65 ± .73	0		1	2.11	1	2.00				
	—	0		2	-.46 ± .12	0		1	-1.60				
C. sabulosa	all	2	.51 ± .13	2	1.17 ± 2.15	0		3	1.24 ± 1.72	7	-0.08	.110	1
	+	0		1	3.32			1	4.58				
	—	0		1	-.98			0					
P. californica	all	5	.97 ± .44	6	.62 ± .69	6	2.18 ± .39	6	1.92 ± .37	22	0.22	.424*	18
	+	3	1.64 ± .44	4	1.43 ± .71	4	2.14 ± .40	5	1.85 ± .45				
	—	0		2	-1.00 ± .33	0		0					
P. badia	all	5	5.72 ± 1.75	5	5.29 ± .62	5	3.29 ± 1.15	7	1.52 ± 1.40	22	-0.77	-.591**	35
	+	3	5.94 ± .72	5	5.29 ± .62	5	3.29 ± 1.15	4	3.06 ± 1.14				
	—	0		0		0		1	-1.40				
N. cinctipes	all	3	.93 ± .99	3	2.60 ± .83	1		1		8	0.04	.034	00
	+	1	2.55	0		0		1	2.83				
	—	1	-.88	0		1	3.13	0					
A. signata	all	4	16.78 ± 8.34	4	4.35 ± .30	4	4.48 ± 3.97	8	-2.14 ± 5.54	20	-2.47	-.622**	39
	+	2	29.20 ± 10.18	0		1	2.25	0					
	—	0		0		0		0					
A. pacifica	all	4	1.26 ± .54	3	.67 ± .25	5	-.38 ± .51	5	.18 ± .43	17	-0.20	-.485*	24
	+	1	2.38	0		1	1.38	0					
	—	1	-.20	0		3	-.94 ± .44	1	-1.14				
C. sabulosa	all	2	1.47 ± .02	2	1.06 ± .75			2	2.86 ± 3.38	6	-2.17	-.307	9
	+	1	1.49	1	1.37			1	6.23				
	—	0		0				0					

†$\bar{m}$ = average percentage in weight/week (m x 100) b
††m = change in rate/degree C
*significantly correlated, $p > .05$
**significantly correlated, $p > .01$

signata in the laboratory was significantly correlated inversely with temperature, but other factors were apparently more important in determining the life span of the other species (Table 4).

The average growth rate of stoneflies kept in the laboratory was considerably less than that of wild ones in the stream, for the species that could be compared, although the fastest growing ones in the laboratory equaled the rate of those in nature. The initial growth rate, for the first two months of life in the laboratory, was greater than later on and was significantly correlated inversely with temperature for *Pa. badia* and *Ar. signata*, about 30 to 40 percent of the effect (r^2 x 100) being attributable to temperature (Table 9). Longer-term growth was less influenced by temperature for these species (Table 9), suggesting that those individuals most affected by temperature did not survive much longer than about two months. Growth of *Ac. pacifica* was similarly affected inversely by temperature, but to a lesser extent (only 24 percent of the effect on initial growth rate being attributable to temperature, Table 9) and apparently not enough to cause early death.

The growth rate of *Ps. californica*, particularly initially, was increased at higher temperatures (Table 11). It was also the longest-lived species in the laboratory (Table 4).

The wide range of responses to the stress imposed by laboratory conditions (including temperature) is remarkable but not unexpected. The Plecoptera observed here came from mountain streams that naturally change considerably from season to season and along their course. Variation in ability to respond to stressful, changing environmental conditions would be of advantage to species living under such conditions: it would reduce the probability that all individuals would be eliminated. Such wide variation means that laboratory experiments such as this should use a large sample size of comparable individuals. It probably is not valid to compare animals from different locations or ones collected at different seasons, and Ludwig (1928) has demonstrated that different stages of development of an insect vary in sensitivity to temperature.

This study suggests that some species (i.e., *Ps. californica*, *Pa. badia*, *Ac. pacifica*, and perhaps *C. sabulosa*) were better suited to long-term observations than were the others. Variables other than temperature had pronounced effects on stonefly growth and fate, and these should be elucidated before further studies are undertaken. The most important of these seem, subjectively, to be water quality, the nature of water movement in the habitat relative to energy expenditure by the animal, suitability of the habitat to the animal's behavior, and (most important) food. The physiological state of individuals is more difficult to assess but must be considered.

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WATER BALANCE AND FLUID CONSUMPTION IN THE SOUTHERN GRASSHOPPER MOUSE, *ONYCHOMYS TORRIDUS*

Vernon C. Bleich[1,2] and Orlando A. Schwartz[1,3]

Abstract.— Weight loss was rapid and fluid consumption decreased sharply when *Onychomys torridus* were exposed to salinities greater than 0.3 Molar. The southern grasshopper mouse is physiologically unspecialized for maintaining water balance in its xeric habitat. The southern grasshopper mouse is capable of weight maintenance on smaller daily water rations than is the northern grasshopper mouse (*Onychomys leucogaster*). Differences in the water balance of *O. torridus* and *O. leucogaster* may influence their local distributions in areas of sympatry.

Previous investigations of water balance in cricetid rodents have included limited information on the grasshopper mice of the genus *Onychomys*. Schmidt-Nielsen and Haines (1964) subjected *O. torridus* to several diets and to increasing concentrations of NaCl solution to test the species's ability to maintain water balance on various regimens. They used body weight maintenance as the criterion for demonstrating water balance. Boice (1972) presented limited data on daily water consumption in *O. leucogaster*, and he cited the lack of other water consumption data for the genus. This investigation was undertaken to partially fill that void and to provide additional information on the water balance of *O. torridus.*

Methods

Six southern grasshopper mice, *O. t. tularensis,* were obtained 18 km north of Reyes Station, San Luis Obispo County, California. The mice were taken to our laboratory and housed in steel laboratory cages (16.5 x 18 x 25.5 cm). A substrate of commercial mineral-type "cat litter" was provided. The temperature was controlled ($\bar{x}=23$ C; range 21-24 C), and the photoperiod was set to coincide with natural conditions. The mice were fed an unsupplemented diet of sunflower seeds *ad libitum* throughout the study.

Our experimental design was modified from that of Schmidt-Nielsen and Haines (1964) and McManus (1972). Water intake was measured using inverted graduated cylinders fitted with angled drinking tubes. A series of controls was used to correct for what little evaporation occurred. Daily fluid consumption was measured to the nearest 0.1 cc. All animals were weighed daily to the nearest 0.1 g.

The mice were exposed initially to *ad libitum* tap water for a three-week period, during which time their weights stabilized. Daily fluctuations of body weights between the second and third week on the tap water regimen were negligible. Salinity (NaCl) was then increased by 0.1 M every other week, from 0.1 M to 0.7 M. The mice were exposed to each successive saline solution for a period of one week. To allow for rehydration, they were given tap water for one week between each successive increase in molarity.

Results and Discussion

Mean body weight and fluid intake varied with increasing salinity (Fig. 1). After the initial stabilization period, weights showed an increase through 0.3 M and then declined sharply. Weight loss continued through 0.6 M, reaching a low value of 57 percent of the initial weights. Four animals died after exposure to 0.6 M NaCl, but two survived rehydration and died after two days' exposure to 0.7 M NaCl. The initial rise in body weight can be attributed to fluid retention. Beyond molarities of 0.3 M, weight loss was rapid, owing to dehydration and decreased food consumption.

Fluid intake increased sharply with exposure to salt concentrations up to 0.2 M. Consumption dropped slightly during exposure to concentrations of 0.3 M and 0.4 M and then dropped sharply through the period of exposure to concentrations of 0.6 M.

The rate of fluid consumption in *O.*

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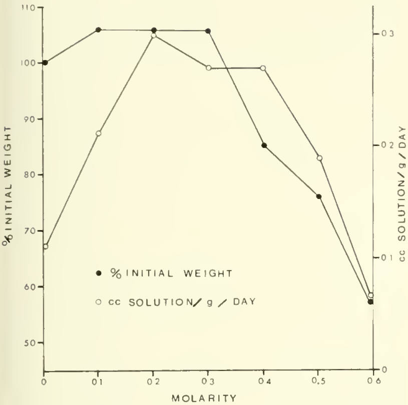

Fig. 1. Water intake and weight of *Onychomys torridus* as functions of NaCl molarity.

torridus showed an initial increase, and then a decrease, probably an avoidance reaction, as McManus (1972) reported for the chinchilla (*Chinchilla laniger*). This initial increase in fluid consumption probably meant that as the kidneys came closer and closer to reaching maximum limits of concentrating capacity, more and more saline water was required from which to extract the same volume of physiologically useful water. Possibly the decrease in fluid consumption at concentrations greater than 0.3 M is attributable to the unpalatability of concentrated salt solutions, as McManus (1972) suggested.

These data indicate that *O. torridus* is an effective osmoregulator when exposed to NaCl concentrations up to and including 0.3 M. Beyond that point, the species is not able to maintain water balance, and it may be unable to survive prolonged periods of exposure to solutions greater than 0.4 M. These results are similar to those reported by Schmidt-Nielsen and Haines (1964). On a diet of laboratory chow and with increasing salinity of the drinking water, all of their *O. torridus* maintained weight on 0.2 M NaCl. Four of the six mice maintained weight on 0.3 M NaCl, and all mice lost weight rapidly on 0.4 M NaCl solution.

Initial rates of consumption of tap water in *O. torridus* allow a comparison with the data of Boice (1972) for *O. leucogaster*. Five mice in this study averaged 0.23 cc/g/day after 20 days. *O. torridus* averaged 0.11 cc/g/day after three weeks. Although possible differences in humidity in the two laboratories were not reported, these data suggest that *O. torridus* is capable of weight maintenance on smaller daily water rations than is *O. leucogaster*. The possibility that differences in the water balance of *O. torridus* and *O. leucogaster* influence their local distributions in areas of sympatry lends itself to further investigation.

The efficiency of *O. torridus* in maintaining body weight on concentrations of NaCl solutions is similar to those of some other myomorph rodents that have been investigated, including *Neotoma micropus* and *Neotoma floridana* (Birney and Twomey, 1970), *Microtus ochrogaster* and *Microtus pennsylvanicus* (Getz, 1963, 1966), *Peromyscus floridanus* (Fertig and Layne, 1963), and *Rattus norvegicus* (Adolph, 1943). All these species lost weight or died at concentrations of 0.3 M NaCl or greater.

The data in our study support the conclusion of Schmidt-Nielsen and Haines (1964) that *O. torridus* is physiologically unspecialized for maintaining water balance in a xeric environment. We concur that the southern grasshopper mouse is adapted to its xeric environment by its carnivorous diet, which provides sufficient moisture for the species to maintain its water balance.

We thank S. Bailey and L. Terzenbach for assistance in the field. J. P. Kinney kindly allowed the use of field facilities at his disposal and gave us permission to trap on private property. C. T. Collins provided the impetus for this study, and we thank him and R. B. Loomis, California State University, Long Beach, for their helpful comments.

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A SYSTEMATIC STUDY OF *COENIA* AND *PARACOENIA*
(Diptera: Ephydridae)

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Abstract.— Shore flies of the genera *Coenia* Robineau-Desvoidy and *Paracoenia* Cresson are revised, resulting in the description of two new subgenera of *Paracoenia, Calocoenia* and *Leptocoenia*, and of four new species, *Paracoenia ampla, P. calida*, and *P. wirthi* from California, and *Coenia alpina* from Labrador, Canada. Biological information on *P. turbida* and *P. calida* is given and the known distribution for each species is presented. *P. paurosoma* is reported from the Palearctic Region for the first time based on specimens from Sweden; several new distribution records from North America are also included. Characters of the male postabdomen are used, and the male genitalia of each species are illustrated. Keys or references to all known species of these genera are included.

Introduction and Review

Shore flies of the ephydrid genera *Coenia* Robineau-Desvoidy and *Paracoenia* Cresson are common and widely distributed in the Holartic region. Typically, flies of both genera are associated with semiaquatic or aquatic environments and many tolerate a diverse range of seemingly inhospitable habitats. They are often abundant around mineral or hot springs, alkaline lakes, and marginal aquatic areas where the water is highly saline. This study was initiated to further the systematic knowledge of these unique flies and to provide a basis for detailed biological investigations.

A synoptic series on the North American Ephydridae was started by Ezra T. Cresson, Jr. (1942, 1944, 1946, 1949), whose papers reviewed most Nearctic genera of the subfamilies Psilopinae, Notiphilinae, and Parydrinae. His untimely death precluded the completion of this series and left the synoptic study of the subfamily Ephydrinae largely unfinished until Sturtevant and Wheeler's review in 1954. This review was the last comprehensive treatment of the genera considered here.

Prior to Sturtevant and Wheeler's paper, the American species of *Coenia* or *Paracoenia* had not been treated together. Coquillet (1902) and Curran (1927) described the first Nearctic species, *Coenia bisetosa* and *C. turbida* respectively, and Johnson (1925) included *C. palustris* (Fallén) in his list of Ephydridae from Massachusetts. Johnson's identification of the latter species as *C. palustris* is questionable, and Sturtevant and Wheeler include this citation under *C. curvicauda* Meigen. After studying the Ephydrinae in the Naturhistorisches Museum, Wien, Cresson (1930) reviewed the European species of *Coenia*. He distinguished *C. curvicauda* from *C. palustris* and designated a lectotype for *C. curvicauda*. Cresson (1935) described a new genus, *Paracoenia*, that included two new species, *platypelta* and *fumosalis*, in addition to *Coenia bisetosa* and *C. turbida*, described previously from North America, and two European species, *C. fumosa* (Stenhammar) and *C. beckeri* (Kuntze). *C. curvicauda* and *C. palustris* were left in the genus *Coenia*. Sturtevant and Wheeler described one additional species, *C. paurosoma*, in their review of 1954.

Cresson delimited *Paracoenia* from other genera based on comparative differences he noted in the dimensions of the head, in the number of dorsocentral bristles (three in *Coenia*, four in *Paracoenia*), and in the presence (*Paracoenia*) or absence (*Coenia*) of well-defined humeral bristles. Most specialists have continued to recognize both *Coenia* and *Paracoenia* as valid genera. Dahl (1959) studied the male genitalia of both genera and suggested that the marked differences between them supported Cresson's view. The two genera were also recognized by Wirth (1965) in the catalog of North American Diptera. Sturtevant and Wheeler, however, recognized only *Coenia*, relegating *Paracoenia* to subgeneric status.

This revision is based primarily upon a comparative study of the male postabdomen and a reevaluation of previously recognized characters. From these studies, I generally concur with Cresson's concept of *Coenia* and *Paracoenia*; however, I now recognize three subgenera in the latter genus, *Paracoenia, Calocoenia*, and

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Leptocoenia. The basis for these proposals will be treated in greater detail in the sections on phylogeny and under the appropriate generic discussions. Four new species are described, three in *Paracoenia* and one in *Coenia.*

Acknowledgments

This study was initially suggested by Dr. Stephen L. Wood while I was an undergraduate at Brigham Young University. Many of the preliminary observations were completed then, although the study has since been expanded as new species were discovered and specimens were examined from a wider geographic area. I thank Dr. Wood for his encouragement and for sponsoring two summers of field work.

Special thanks are extended to Dr. Paul H. Arnaud, California Academy of Sciences, to Dr. Willis W. Wirth, Systematic Entomology Laboratory, ARS, USDA-National Museum of Natural History, Washington, D.C., and to Mr. Guy E. Shewell, Canadian National Collection of Insects, for their extensive cooperation and assistance.

Type specimens were borrowed from the Academy of Natural Sciences of Philadelphia (Drs. David C. Rentz and Selwyn S. Roback); the National Museum of Natural History (Dr. W. W. Wirth); and the Museum of Comparative Zoology (Mrs. Janice C. Scott and Dr. John F. Lawrence).

In addition to the above, the following institutions and curators kindly loaned specimens, without which this study could not have been completed: University of Minnesota (Dr. Philip J. Clausen); Kent State University (Dr. B. A. Foote); University of California, Riverside (Dr. Saul I. Frommer); Los Angeles County Museum of Natural History (Dr. Charles L. Hogue); Iowa State University (Dr. Robert E. Lewis); Cornell University (Dr. L. L. Pechuman); University of California, Davis (Dr. R. O. Schuster); Washington State University (Dr. William J. Turner); Florida State Collection of Arthropods (Dr. Howard V. Weems, Jr.); and Brigham Young University (Dr. Stephen L. Wood). Dr. Marshall R. Wheeler generously loaned specimens from his private collection.

I also wish to gratefully acknowledge Drs. John D. Lattin, Carol A. Musgrave, Paul Oman, and Paul O. Ritcher, Oregon State University, for their technical and editorial assistance and for many stimulating discussions on systematics. The stereoscan electron micrograph was taken by Mr. Alfred Soeldner, Oregon State University. Dr. Willis W. Wirth, USDA-USNM was also kind enough to review this study.

Methods and Discussion of Characters

All observations were made using a stereomicroscope; a filar micrometer was used for the measurements. Morphological characters, especially those of the male postabdomen, were illustrated using an ocular grid. All illustrations were drawn to the same scale on mylar drafting film. Preparation of the male or female postabdomen for study involved its removal and heating in a 10 percent sodium hydroxide solution to remove extraneous tissue. The abdomen was then washed, further dissected, and compared. For permanent storage the abdomens were preserved in plastic microvials filled with glycerin and attached to the appropriate specimen.

During the course of the study, I examined approximately 4,000 specimens, including the type specimens of all but *Coenia curvicauda,* and I did examine European specimens of this species. The type specimens examined formed the basis for the species descriptions.

Species descriptions are purposefully brief; for the most part they summarize specific differences or additions not found in the more detailed generic descriptions. The diagnoses will differentiate the species from similar taxa. For previously recognized species, the descriptions also contain any newly acquired information for comparative purposes. Polymorphic and polytypic variations are included under remarks.

Characters considered in this study are from all body tagma and have been quantified where appropriate. Ratio values are based on an average of ten specimens selected because of obvious size differences.

Head.— *Eye-to-cheek ratio.* This is the ratio of genal height to eye height. Measurements are taken from the head in profile. This ratio is a convenient character for some species groups.

Width–to–height ratio. This ratio is calculated as head height to head width; measurements are made from a cephalic orientation.

Eye-width–to–face-length ratio. This ratio is based on measurements from the head in profile and is calculated as face length to eye width.

Height–to–length ratio. This is the ratio of the height of the head in profile to its length, measured from the most anterior surface of the face to the posterior margin of the eye. Cresson first used this character when describing *Paracoenia.*

Aristal pectinations. The length of the pectinate branches on the dorsum of the arista is compared with the base width of the arista. This character is sometimes difficult to use and is best seen in well-preserved specimens.

Interfoveal hump and marginal bristles. This character is correlated with the eye-to-cheek ratio. It is the comparison of the hump height to the length of the bristles along the oral margin. Hump height is related to genal height.

Facial color. This character is subject to considerable variation in many species, especially species of *Paracoenia*, but it is of some diagnostic value in others. The species of *Coenia* and *Calocoenia* have relatively constant facial color.

Postocular bristles. The development of the dorsalmost postocular bristles is useful in distinguishing *Paracoenia* from *Coenia.*

THORAX.— *Acrostichal hairs.* The arrangement and degree of development of the acrostichal hairs have been overlooked as a diagnostic character other than at the species level. These characters are important in distinguishing the subgenera of *Paracoenia.*

Dorsocentral bristles. The number of dorsocentral bristles has been extensively used as a major character and was accorded significance at the generic level by Cresson.

Humeral bristles. The presence or absence of well-developed humeral bristles also was used by Cresson to delimit these genera. I have followed Cresson in attributing generic importance to this character as well as to the number of dorsocentral bristles.

Halters. The color of the halters can be used to distinguish some groups of species. Cresson (1930) mentioned that this character is usually variable and is not important as a key character.

Costal vein ratio. This is the ratio of distance along the coastal margin between R_1 and R_{2+3} to the distance between R_{2+3} and R_{3+4}. All measurements are the maximum straight-line distances.

M_{1+2} ratio. This is the ratio of the distance of the M_{1+2} anterior to the posterior cross vein to the distance posterior to the posterior cross vein.

Costal bristles. The presence or absence of costal bristles along the dorsal and/or ventral surface is diagnostic of some genera. *Calocoenia* is the only taxon of Scatellini with prominent bristles on both surfaces, a character found in many species of Ephydrini.

Femoral comb. The femoral comb is a sexually dimorphic character restricted to the males of *Paracoenia* s. str.

ABDOMEN.— *Male postabdomen.* The male genitalia previously have not been used as characters at the species or generic level; I have found them extremely useful at both levels. These characters are discussed more fully in the generic and specific descriptions.

Female ventral receptacle. The shape of this structure seems to be of considerable diagnostic value, especially at the generic level.

PHYLOGENY AND CLASSIFICATION

Both *Coenia* and *Paracoenia* belong to Scatellini as it is presently characterized. The tarsal claws are curved and short, and the pulvilli are developed normally. The tribal concepts, however, have not been reassessed since Wirth (1948, 1970, 1971), Oliveira (1954a, 1954b, 1957), and others (Collin, 1963; Steyskal, 1970) began incorporating characters of the male postabdomen in their treatments of various Ephydrinae genera. This is especially evident with the annectant genus *Austrocoenia* Wirth from South America as well as several undescribed genera from the neotropics, which will require further evaluation before a reliable classification of the higher categories can be achieved. Biological information and systematic studies of the immature stages would also be most useful.

Because biological and morphological data of the larvae are lacking in many related genera and in some of the taxa herein considered, I have elected to recognize a conservative classification in this study. Taxa above the species level but within the generic limits of *Paracoenia* as Cresson described it are given subgeneric status. But this status is provisional, awaiting the accumulation of additional information as outlined above and further assessment.

The subgenera of *Paracoenia* are primarily based on characters of the male postabdomen and correlated external features. The resulting concepts are sufficiently distinct to be easily recognizable as delimited in the diagnoses and as seen by reviewing the figures. *Paracoenia* (*Paracoenia*), for example, is the largest subgenus with eight species, yet each known taxon belonging to this category can be readily placed without difficulty. Further, most of the diagnostic characters are apomorphus and define monophyletic groups.

On the other hand, the relationships between subgenera are somewhat obscure and the generic concept is not as neatly circumscribed. More reliance is placed on chaetotaxy characters of doubtful significance. However, coupled with our meager knowledge regarding biology, habitat, etc., I feel that the genus is convenient and does reflect a cohesive unit.

Coenia has only three species, all of which are evidently closely related. Except by association with males and in some instances with locality, the females of one species are generally indistinguishable from those of another. Similarly, the males closely resemble each other, although their genitalic characters are consistent and constant, a fact that facilitates identification and classification. This group in particular needs biological study.

TAXONOMY

Key to *Coenia* and *Paracoenia*

1. Four pairs of dorsocentral bristles; humeral bristles well developed; dorsalmost postocular bristles subequal to verticals .... *Paracoenia* Cresson

Three pairs of dorsocentral bristles; no developed humeral bristles; dorsal postocular bristles much smaller than verticals .... *Coenia* Robineau-Desvoidy

Genus *Paracoenia* Cresson

Paracoenia Cresson, 1935, Trans. Amer. Ent. Soc. 61:356. Type-species, *Coenia bisetosa* Coquillett, by original designation. Sturtevant and Wheeler, 1954, Trans. Amer. Ent. Soc. 79:164-166 (review of Nearctic species as subgenus of *Coenia*). Wirth, 1965, USDA Agricultural Handbook No. 276, pp. 755-756 (catalog).

DIAGNOSIS.— Members of this genus are similar to those of *Coenia* but can be distinguished from the latter as follows: Postocular bristles immediately posterior to the vertical bristles subequal to verticals; at least one humeral bristle well developed, much larger than the surrounding setae; four pairs of dorsocentral bristles.

DESCRIPTION.— Small to large, length 2.1 to 4.4 mm, females usually larger than males; dark species, often with subshining metallic reflections; head with characteristic arched prefrons.

Head. Front (postfrons) rectangular, wider than long; margins of mesofrons directed inward anteriorly; mesofrons subshining with metallic reflections, setulose; ocellar triangle equilateral, concolorous with fronto-orbital areas, dull, microsculptured. One large pair of proclinate diverging ocellar bristles; postvertical bristles various; two pairs of fronto-orbital bristles; both inner and outer vertical bristles well developed; two pairs of strong postocular bristles immediately posterior to vertical bristles. Antennae dark brown to black, pollinose; second segment setulose, especially on median and ventral surfaces; dorsum of arista pectinate, pectinate branches up to three times the width of aristal base, sometimes equaling third antennal segment width. Pruinose face (prefrons) protruding, arched with interfoveal hump, setulose; setae descending from hump and along ventral margin strongest. Eye suboval; gena variously developed with genal bristle toward ventral margin. Mouthparts dark; prementum large, bulbous.

Thorax. Dorsum of mesonotum subshining to dull, generally concolorous, sometimes with discernible median and lateral stripes. Acrostichal hairs in approximately six irregular rows to two distinct rows; four pairs of dorsocentral bristles; one pair of intra-alars; two to three pairs of humeral bristles; two pairs of notopleurals; one pair of presuturals; one pair of supra-alars; two pairs of post-alars; dorsum of scutellum convex to flat, setulose; at least two well-developed pairs of lateral scutellar bristles; one pair each of mesopleural and sternopleural bristles. Wings transparent to infuscated; costal setae weak to strong, on dorsal and/or ventral margins. Legs dark, pollinose to subshining.

Abdomen. Abdomen of males with five visible tergites, females with six to seven, subshining to pollinose; most species with pollinose band near the posterior margin of each tergite; fifth abdominal tergite of males with anteroventral projection in some species of *Paracoenia* s. str. Female postabdomen with three complete segments, six, seven, eight; ninth segment with tergite not fused dorsally, with one pair of long spines on ventral margin; sternite of ninth segment also with one pair of spines; female abdomen terminating with cerci. Ventral receptacle variously shaped. Male postabdomen symmetrical, reduced; sixth segment with spiracles only although European species of *Paracoenia* s. str. have a transverse sclerotized band posterior to fifth sternite which could represent sixth sternite; seventh and eigth segments absent. Spiracles one through six present, sixth spiracle in membrane between fifth abdominal tergite and epandrium, all other spiracles in ventral margin of respective tergites. Epandrium suboval with scattered setae; dorsum of epandrial plate bearing two setulose cerci; ventrally epandrium terminates at juncture with prominent, projecting surstyli of various shapes. Hypandrium extending dorsally and ventrally, attaching to epandrium, lateral hypandrial process sheathing aedeagus; aedeagus well sclerotized, pointed apically.

DISCUSSION.— For purposes of classification the species of *Paracoenia* are arranged in three subgenera, *Paracoenia*, *Calocoenia*, and *Leptocoenia*. The latter two subgenera might be accorded generic status by future revisers since the male postabdomens and other characters are fairly distinctive. But before the generic classification of these taxa is assessed, the higher classification of the subfamily Ephydrinae should be revised on a worldwide basis to insure consistency in generic concepts, especially the distinguishing gap. Such a review will necessarily entail a great deal of descriptive work because of our spotty knowledge of many faunal areas, i.e., the Neotropical Region, which are replete with undescribed species.

The following key works best for male specimens and includes both European species. Illustrations of the male genitalia will facilitate accurate identification.

Key to *Paracoenia* subgenera and species

1. Acrostichal hairs in two rows; dorsum of scutellum slightly convex to flat; posteroventral margin of mesofemora without row of comblike bristles in males 2

Acrostichal hairs in four to six irregular rows; dorsum of scutellum convex; posteroventral margin of mesofemora with dense row of bristles in males .... subgenus *Paracoenia* Cresson 3

2. Length over 3.25 mm; eye–to–cheek ratio 1:0.25 or larger; well-developed costal bristles projecting anteriorly from ventral and dorsal surfaces .... subgenus *Calocoenia*, *Caloceonia platypelta* (Cresson)

Length under 3.00 mm; eye–to–cheek ratio 1:0.25 or less; bristles along costal margin not developed .... subgenus *Leptocoenia*, *Leptocoenia paurosoma* (Sturtevant and Wheeler)

3. Fifth abdominal sternite of male deeply U-shaped, Figs. 11, 12; Palearctic 4

Fifth abdominal sternite broadly U-shaped, Figs. 1-6; Nearctic 5

4. Length approximately 5 mm; dorsum of thorax and abdomen grayish-blue to light brown, dull; pleura gray .... *P. beckeri* (Kuntze)

Length usually less than 4 mm; thorax and abdomen darker, bluish-olive green to greenish-gray; subshining dorsally .... *P. fumosa* (Stenhammar)

5. Postocellars small, no longer than their distance apart at base; facial pruinosity yellowish-gold with greenish-blue metallic reflection showing through around interfoveal hump; ventral projection of fifth abdominal tergite in males blunt, parallel to remainder of ventral margin .... *P. fumosalis* Cresson

   Postocellars larger, longer than their distance apart at base, facial pruinosity various; ventral projection of fifth abdominal tergite absent or not as above 6

6. Process of fifth abdominal tergite in males not developed 7

   Process of fifth abdominal tergite developed into a projection of various shapes 8

7. Subshining with metallic blue reflections; eye–to–cheek ratio 1:0.45 or larger; associated with hot sulfur springs .... *P. calida* n.sp.

   Subshining with metallic green reflections; eye–to–cheek ratio 1:0.3 or less; associated with thermal or cool water .... *P. turbida* (Curran)

8. Process of fifth abdominal tergite of male broadly produced; acrostichal hairs few; male genitalia as in Fig. 1; presently known only from vicinity of Los Angeles, California .... *P. ampla* n. sp.

   Process of fifth abdominal tergite not as broadly produced; acrostichal hairs stronger; surstyli of male genitalia not pointed distally or bare 9

9. Surstyli thickened basally, at least one-half total length; sheathing projection of hypandrium broadly rounded apically; smaller, length 3.1–3.6 mm; setation less well developed, especially on face and mesonotum; male genitalia as in Fig. 6 .... *P. wirthi* n. sp.

   Basal expansion of surstyli less than one–third total length; lateral process of hypandrium pointed; length 3.7–4.4 mm; facial and mesonotal hairs well developed .... *P. bisetosa* (Coquillett)

Subgenus *Paracoenia* Cresson

Paracoenia Cresson, 1935, Trans. Amer. Ent. Soc. 61:356. Type-species *Coenia bisetosa* Coquillett, by original designation. Sturtevant and Wheeler, 1954, Trans. Amer. Ent. Soc. 79:164-166.

Diagnosis.— This subgenus is similar to *Calocoenia* but may be distinguished as follows: acrostichal hairs in several irregular rows, no prominent hairs; dorsum of scutellum convex; costal setae weak, in a single row; posteroventral margin of mesofemora with distinct row of bristles in males; many species with an anteroventral projection of the fifth abdominal tergite; epandrium of male with an anteromedian triangular projection; aedeagal apodeme subquadrate.

Description.— Moderately large, length 3.1–5.0 mm; dark species, often with subshining metallic reflections.

Head. Front rectangular; mesofrons subshining to shining with metallic reflections; pectinate branches of arista up to three times the width of aristal base, often equaling third antennal segment width. Face with prominent interfoveal hump, strongly arched; eye–to–cheek ratio usually 1:0.22-0.45; width–to–height ratio 1:0.67; eye–width–to–face–length ratio 1:0.45 (1:0.85 in *P. calida*); height–to–length ratio 1:0.93.

Thorax. Dorsum subshining although subdued in aged specimens, generally shining more posteriorly. Acrostichal hairs in four to six irregular rows; otherwise chaetotaxy as in generic description; scutellum convex. Costal vein ratio 1:0.2; M_{1+2} vein ratio 1:0.90; costal setae generally weak, developed setae on dorsal margin only. Mesofemora of males with posteroventral row of comblike bristles.

Abdomen. Subshining to pollinose, if shining, reflection somewhat less than dorsum of scutellum. Female ventral receptacle with operculum, wider than high, extending process not longer than operculum length. Surstyli of male postabdomen projecting from lateral margins of epandrium, long, variously shaped; a triangular process lies between surstyli, some species, with a median groove (see figures of included species).

Discussion.— The species included in

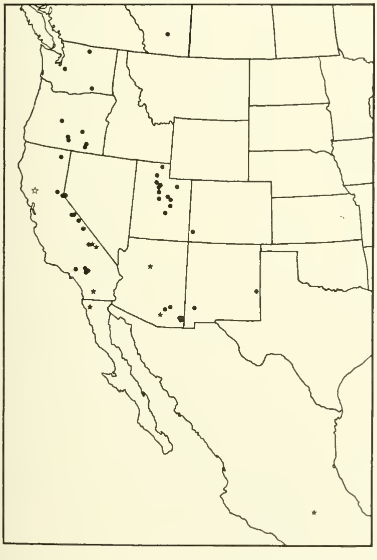
this taxon form a fairly homogeneous group based mostly on apomorphous characters (see diagnosis). The joint possession of these characters delimits the monophyletic grouping here understood as *Paracoenia* s. str. and determines the subgeneric concept. Two species previously included here, *P. paurosoma* (Sturtevant and Wheeler) and *P. platypelta* Cresson, are sufficiently distinct to form the basis for new subgenera.

Paracoenia s. str. is Holarctic, but no one species is presently known to occur in both Eurasia and North America. However, many species of the subgenus are widely distributed, and it is not uncommon to collect two or more species from the same general locality. Other species such as the Nearctic *P. calida* and *P. ampla* and the Palearctic *P. beckeri* are known only from very localized geographic areas.

The subgenus contains eight species; six are Nearctic and two are Palearctic. All of the Nearctic species except *P. fumosalis* are found principally in western North America. A more detailed zoogeographic account, aside from the general distributions indicated under the appropriate species, will not be possible until more collection data become available.

The paucity of biological studies precludes a detailed accounting for the entire subgenus. For the Nearctic region, only *P. turbida* has been studied in any detail (Brock et al., 1968, 1969). However, Dr. B. A. Foote and associates at Kent State University and Dr. Karl W. Simpson of Cornell University are currently engaged in studies of various ephydrid species that will greatly enhance our biological knowledge.

Most species can tolerate harsh environments, especially aquatic habitats with high concentrations of various salts. These shore flies are often abundant, for example, along the margin of Great Salt Lake or associated with hot sulfur springs in Yellowstone National Park, Wyoming. Scheiring and Foote (1973) further report finding larvae in the shoreline mud of alkaline lakes and in sewage-impregnated mud. The larva and pupa of *P. fumosa*, a Palearctic species, were described by Beyer (1939).



Map 1.— Distribution of *Paracoenia wirthi*, filled stars; *Paracoenia platypelta*, filled circles; *Paracoenia ampla*, open circle; and *Paracoenia calida*, open star.

Paracoenia (*Paracoenia*) *ampla*, n. sp.

Fig. 1, Map 1

Diagnosis.— Although this species is quite similar to *P. bisetosa*, it can be readily distinguished from the latter by comparing male postabdomens. The surstyli of *P. ampla* are sinuate, bare, and strongly narrowed apically. Further, the shape of the lateral hypandrial process is distinctive, especially the clavate extension. This species is larger than most *P. bisetosa* and in general is less setulose. The acrostichal hairs, in particular, are weak and widely scattered.

Description.— Length approximately 4.0 mm (the abdomen was removed for dissection before measurements were taken); generally subshining with bluish-green metallic reflections.

Head. Width-to-height ratio 1:0.7; height-to-length ratio 1:1; eye-width-to-face-length ratio 1:0.44; facial pruinosity brownish-gold.

Thorax. Setae generally weak, scattered; costal vein ratio 1:0.17; M_{1+2} ratio 1:1.

Abdomen. Fifth tergite ventrally produced into broadly based processes that extend anteriorly to basal margin of fused

U-shaped fourth and fifth abdominal sternites, processes pointed apically; fifth abdominal sternite thin, weak, deeply U-shaped with parallel arms; epandrium subquadrate; medial triangular projection proportionately small to epandrial size; surstyli directed inward, apically narrowed, sinuate, bare; hypandrium in profile almost rectangular, with extending process slightly clavate; aedeagus broad basally, tapering rapidly, curved and pointed apically. Male genitalia as in Fig. 1.

Distribution.— Los Angeles, California.

Types.— Male holotype with the following label data: Los Angeles, Cal., Apr 29th, 1915, M. VanDuzee; a determination label, *Coenia bisetosa* Coq., 1919, Cresson; a blue M C VanDuzee collection label. The type will be deposited with the California Academy of Sciences, type number 12032.

Remarks.— This species is known only from the unique male holotype. Recognition of the specimen as representing a new species is justified in view of the very distinctive male postabdomen. Unfortunately, *P. ampla* may already be extinct due to the tremendous and rapid urban growth in the Los Angeles area since 1915. I have examined several *Paracoenia* specimens from Los Angeles County but none were *ampla*.

Paracoenia (*Paracoenia*) *bisetosa* (Coquillett)

Fig. 4, Map 3

Coenia bisetosa Coquilllett, 1902, J. N. Y. Ent. Soc. 10:183

Caenia [sic] bisetosa: Aldrich, 1905, Smithson. Misc. Coll. 66(1444):631

Paracoenia bisetosa: Cresson, 1935, Trans. Amer. Ent. Soc. 61:356

Coenia (*Paracoenia*) *bisetosa*: Sturtevant and Wheeler, 1954, Trans. Amer. Ent. Soc. 79:164

Types.— Male holotype, Salt Lake, Utah, 25 June, E. A. Schwarz collector. The type is deposited with the National Museum of Natural History, Washington, D.C., type number 6644. This specimen is in relatively good condition, although the wings are ragged and torn.

Diagnosis.— *P. bisetosa* is similar to *P. turbida*, but the former is larger, more setulose, and more brownish. The posterior margin of the fifth abdominal sternite is sclerotized and of uniform thickness throughout. The ventral process of the fifth abdominal tergite is well developed and pointed. Basally, the surstyli are enlarged but narrow quickly, making the lateral margin sinuate. The hypandrial process usually tapers evenly to a rounded point. Outwardly, this species might be confused with *P. ampla*, but the male genitalia of *P. bisetosa* differ sufficiently from the latter that recognition of either species should not be difficult.

Description.— Length 3.7-4.4 mm; dark greenish-brown dorsally; laterally quite pollinose.

Head. Mesofrons with bronze metallic reflections. Eye-to-cheek ratio 1:0.34; width-to-height ratio 1:0.69; height-to-length ratio 1:0.9; eye-width-to-face-length ratio 1:0.5.

Thorax. Dorsum with pollinose anterior, becoming subshining posteriorly; pleural areas largely pollinose. Wings infuscated with light brown.

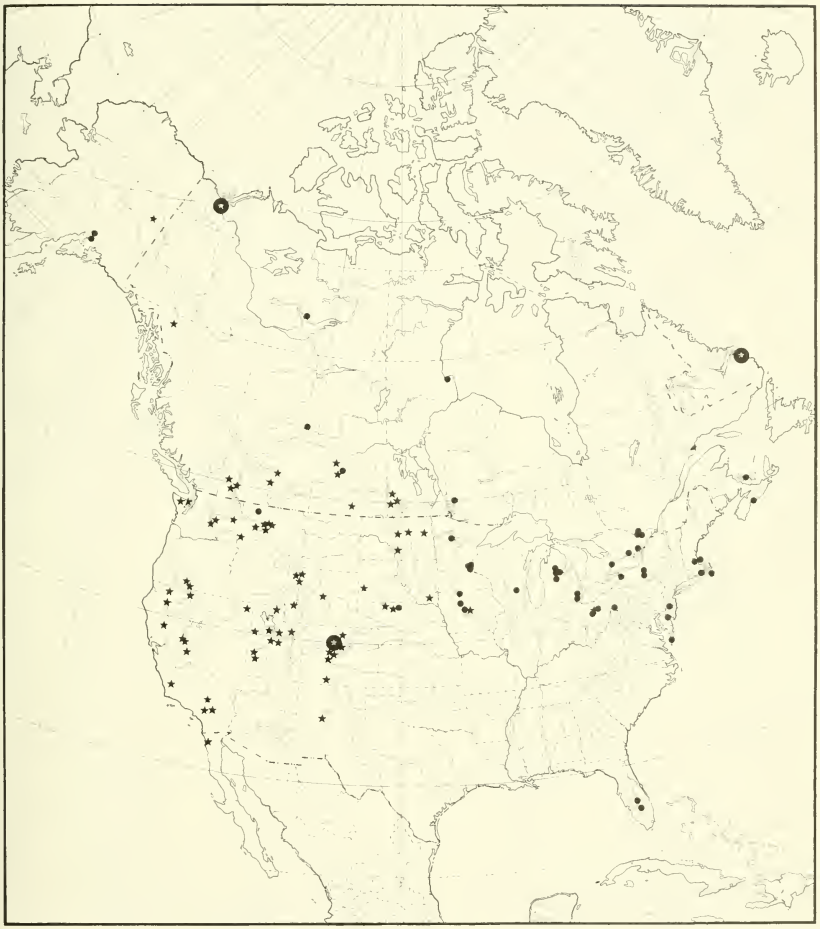
Abdomen. As in diagnosis and Fig. 4.

Specimens examined.— 1881.

Distribution.— Like *P. turbida*, this species is primarily a western North American taxon, although collecting data indicate eastern extensions to New York (5 miles W Cardiff), Pennsylvania (Philadelphia), Delaware (Bombay Hook), and Virginia (Saltville). The Northwest Territories (Nyarling River), Canada, is the northernmost collection site, and the species ranges from there southward through most of the Midwest to Texas (Buffalo Spring Lake) and into Mexico (Guadalupe Can., B. Calif.). Westward, specimens have been collected in every state and Canadian province west of the 100th parallel.

Remarks.— This is the most common species of the genus and among the most widespread. It is also one of the most variable. Facial pruinosity color runs from bright brownish-orange to silver, and the general body color varies from shining greenish-brown to a subdued, grayed green. Age polymorphism is also apparent; older specimens are often more brownish and are worn.

Dr. Willis W. Wirth has made several collections of *P. bisetosa* from aquatic habitats with varying concentrations of both alkaline and saline salts.



Map 2.— Distribution of *Paracoenia fumosalis*, filled circles; *Paracoenia turbida*, filled stars; and *Coenia alpina*, enclosed stars.

Paracoenia (*Paracoenia*) *calida*, n. sp.

Fig. 3, Map 1

Diagnosis.— This is the most distinctive Nearctic species and is easily separated from all others of the genus. Externally, the blue metallic reflections from the dorsum, the protruding prefrons, and the eye-to-cheek ratio are diagnostic. The male postabdomen resembles that of *P. bisetosa* but differs in the shape of the hypandrial process, which is more or less of uniform thickness and has a noticeable taper just before the apices. Additionally, the fifth abdominal tergite does not have a ventral extension, although the margin is pointed. *P. calida* and *P. bisetosa* are approximately the same size.

Description.— Length 3.4-4.3 mm, holotype male 3.9 mm, generally dark, gray pollinose on head and thoracic plurae with subshining blue metallic reflections dorsally.

Head. Eye-to-cheek ratio 1:0.45; height-to-length ratio 1:1; width-to-height ratio 1:0.71; eye-width-to-face-length ratio 1:0.85. Fronto-orbital and ocellar triangle areas blackish-gray, concolorous with margins of frons; postocellar bristles weak in some specimens; pruniose face grayish-tan.

Thorax. Pleural areas dull, pollinose; dorsum subshining to shining, brownish-blue; halters dark, reddish-brown to black; wings completely infuscated, brown to smoky. Tarsal claws well developed, as long as third or fourth tarsomere; pulvillar pads proportionately small to claw size.

Abdomen. Dorsum of all segments with distinct blue to purplish-blue reflections, reflections stronger in general than elsewhere on body; ventral margin of fifth abdominal tergite broadly pointed, without lobelike projection; fifth abdominal sternite broadly U-shaped, narrow projecting arms forming obtuse angle; setae along posterior margins of tergites much larger than rest of setae, at least twice as long, in some female specimens three to four times as long. Surstyli of male genitalia with more or less gradual taper, not sinuate or pedunculate; aedeagus short; hypandrial process as described in diagnosis.

Distribution.— Wilbur Hot Springs, Colusa Co., California.

Types.— Male holotype, allotype, and all paratypes are from the type locality. Two male and 9 female paratypes, H. J. Jacob; 1 male and 1 female paratype, 27 June 1950, L .W. Quate; holotype, allotype, and 205 male and 96 female paratypes, 25 June 1974, W. N. Mathis, Primary types will be deposited with the U. S. National Museum of Natural History, type number 72975. Male and female paratypes will be deposited with the California Academy of Sciences, Canadian National Collection, Academy of Natural Sciences of Philadelphia, Kent State University, Washington State University, and Oregon State University. The remaining paratypes are in my collection.

Remarks.— Of all the Nearctic species of *Paracoenia* s. str., *P. calida* is perhaps the most remarkable. Its known distribution is limited to a hot sulfur spring in the foothills just east of Clear Lake, California. The larvae develop and mature in all but the hottest water where they can easily be collected in great numbers. The adults are also abundant and were often observed to congregate in large clumps near the spring source where shaded or protected areas could be found. Empty puparia that are scattered on the surface of the effluent and along its margins are often utilized as oviposition sites. Figure 13 is a stereoscan electron micrograph of the egg of *P. calida.*

The effluent of the spring emptied into a small creek around which swarming numbers of other ephydrids were encountered on emergent grasses and in quieter eddies on the water's surface. *P. calida*, however, was not common there, and only an occasional collection was made away from the hot springs. It is also of interest that a new saldid species was recently described from the same locality (J. T. Polhemus, 1967).

The specific name, *calida*, is descriptive of the habitat.

Paracoenia (*Paracoenia*) *fumosalis* Cresson

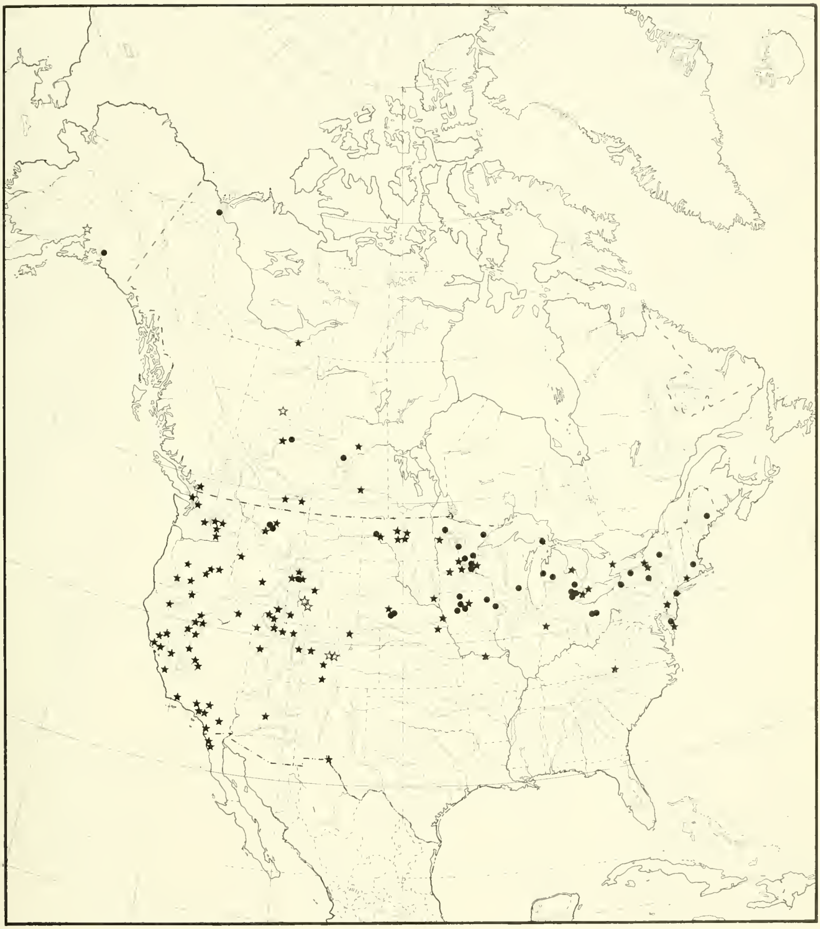
Fig. 2, Map 2

Paracoenia fumosalis Cresson, 1935, Trans. Amer. Ent. Soc. 61:356

Coenia (*Paracoenia*) *fumosalis*: Sturtevant and Wheeler, 1954, Trans. Amer. Ent. Soc. 79:164

Types.— Male holotype, Rockport, Massachusetts, 28 August 1913, C. W. Johnson collector. The type is deposited with the Boston Natural History Society (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts), type number 31759. One male and two female paratypes are topotypical. Four female paratypes were collected on Nantucket Island, 13 July 1926 by C. W. Johnson. All paratypes are deposited with the Academy of Natural Sciences of Philadelphia.

Diagnosis.— Cresson (1935) stated that this species is similar to *P. bisetosa* and *P. fumosa*, which is Palearctic. My observations agree with Cresson's, although in many respects *P. fumosalis* is unique among *Paracoenia* species. The males are most easily distinguished from similar taxa by the rounded, fingerlike projection of the fifth abdominal tergite. This process is parallel to the ventral margin of the tergite that is deeply incised and of uniform thickness before the slightly enlarged, rounded apex. The fifth abdomin-



Map 3.— Distribution of *Paracoenia bisetosa*, filled stars; *Coenia paurosoma*, open stars; and *Coenia curvicauda*, filled circles.

al sternite is subrectangular without extending arms from the posterolateral margins. The surstyli are narrowly S-shaped, and the median triangular process often has a median groove that is cleft apically. The hypandrial process is much longer than the aedeagus, and apically it is truncate. Externally, *P. fumosalis* differs from all others in the length of the postocellar bristles, which are usually shorter than their distance apart at the base. Further, the tannish-bronze color of the pruinose face seems to be constant.

Description.— Length 3.5-4.0 mm; dark brown, lightly pollinose to subshining dorsally; some greenish-blue metallic reflections.

Head. Mesofrons shining with bluish reflections; fronto-orbital areas subshining brown; face concolorous with mesofrons, pruinose, tannish-bronze. Eye-to-cheek ratio 1:0.3; width-to-height ratio 1:0.64;

height-to-length ratio 1:0.87; eye-width-to-face-length ratio 1:0.41.

Thorax. Dorsally subshining, purplish-blue reflections, dark brown. Pleural areas pollinose except dorsal margin. Wings infuscated with brown.

Abdomen. Concolorous with dorsum of thorax. Male postabdomen as in diagnosis and Fig. 2.

Specimens examined.— 368.

Distribution.— *P. fumosalis* is predominately a notheru and eastern North American species. I have examined material from Alaska (Matanuska and Eagle River flats) and from all of the Canadian provinces except British Columbia and the Yukon Territory. In the continental United States, *P. fumosalis* ranges westward to Montana (Libby), eastward through the Great Lake states, some midwestern states (Nebraska, Iowa), and into the Northeast. It has also been collected as far south as Florida (Archbold Biological Station, Lake Placid), and it presumably occurs between Florida and the Northeast. Wirth (1965) lists California as the westernmost extension of *P. fumosalis*, but I have not seen specimens from California.

Remarks.— Examination of over 350 specimens of this species from a wide selection of localities within its distribution revealed very little morphological variation. This species is very uniform except for slight artificial size differences reflecting the mode of preservation. The facial coloration seems to be a consistent diagnostic character unlike other widespread species of *Paracoenia.* I suspect that the species is quite vagile and that the apparent uniformity is due to extensive genetic exchange.

Although I do not know of any localities in which this species is associated with hot springs, it has been collected around alkaline and saline habitats. Scheiring and Foote (1973) reared specimens and report finding larvae in mud impregnated with organic sewage.

Paracoenia (*Paracoenia*) *turbida* (Curran)

Fig. 5, Map 2

Caenia [sic] turbida Curran, 1927, Can. Ent. 59:91

Coenia (*Paracoenia*) *turbida*: Sturtevant and Wheeler, 1954, Trans. Amer. Ent. Soc. 79:165

Paracoenia turbida: Wirth, 1965, USDA Agri. Handbk. No. 276:756

Types.— Male holotype and allotype, Old Faithful, Yellowstone National Park, Wyoming, 30 September 1924, N. Criddle. Two male and one female paratype have the same label data as the type. All types are deposited with the Canadian National Collection, type number 2370.

Diagnosis.— Externally, this species resembles *P. wirthi* and is sometimes confused with *P. bisetosa.* However, it differs from both in the shape of the hypandrial process, which apically narrows more abruptly although the apex is rounded. Also, the lateral margins of the surstyli do not taper apically as rapidly as *P. bisetosa* nor are they enlarged basally as in *P. wirthi.* Outwardly, *P. turbida* is smaller than *P. bisetosa* but of approximately the same length as *P. wirthi.* However, the acrostichal hairs are weaker in *turbida.* The fifth abdominal sternite is more similar to that of *bisetosa,* although the more sclerotized posterior margin is not as wide nor as uniform in thickness as it is in *bisetosa.*

Description.— Length 3.25-3.75 mm; dark greenish-brown, subshining dorsally.

Head. Fronto-orbital areas dark brown, pollinose to subshining. Eye-to-cheek ratio 1:0.3; width-to-height ratio 1:0.65; height-to-length ratio 1:0.93; eye-width-to-face-length ratio 1:0.44.

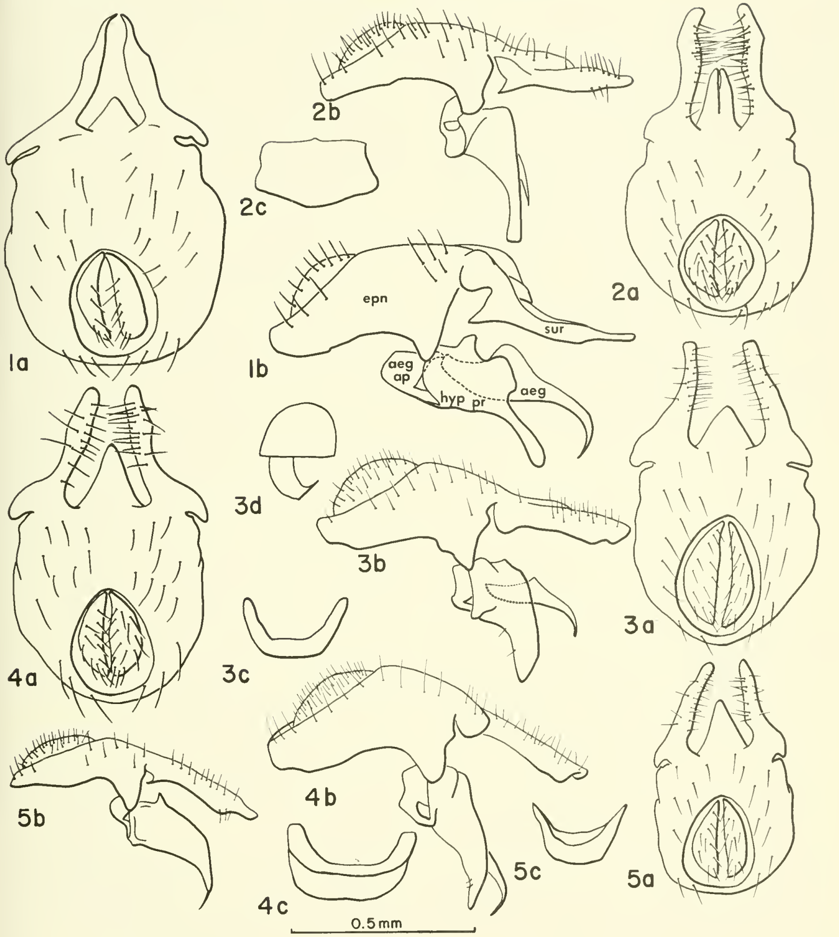
Thorax. Anterior area of dorsum slightly pollinose, becoming subshining to shining posteriorly; pleural areas in general more subdued than dorsum, especially along margins. Wings nearly transparent to light brown.

Abdomen. As in diagnosis and Fig. 5.

Specimens examined.— 674.

Distribution.— The majority of collection localities are west of the Rocky Mountains, although they do extend east to Nebraska (Cherry Co., Big Alkali Lake), Iowa (Ames), and Ohio (Kent, 5.6 miles SE). Specimens have been collected as far north as Alaska (Circle Hot Springs) and southward through Canada (British Columbia to Manitoba) and the western United States into Mexico (60 km S Tijuana).

Remarks.— Strength of setation, general body color, especially the facial pruinosity, and overall size show considerable variability. Polymorphism within a sin-



Figs. 1-5.— Male and female genitalia. 1 a,b *Paracoenia ampla,* 2 a,b,c *Paracoenia fumosalis;* 3 a,b,c,d *Paracoenia calida;* 4 a,b,c *Paracoenia bisetosa*; 5 a,b,c *Paracoenia turbida.* Fig. a, ventral view of cerci, epandrium, and surstyli; Fig. b, lateral view of cerci, epandrium (epn), surstyli (sur), aedeagal apodeme (aeg ap), hypandrial process (hyp pr), and aedeagus (aeg); Fig. c, ventral view of male fifth abdominal sternite; Fig. d, lateral view of female ventral receptacle.

gle population of *P. turbida* seems to vary as greatly as the total species variance. Character displacement was not apparent in areas where *turbida* occurs sympatrically with other *Paracoenia* species.

Brock, et al. (1968, 1969) have studied the biology of *turbida* from near the type locality in Yellowstone National Park, Wyoming. They found that both larvae and adults feed on blue-green algae and the filamentous bacteria of mucilaginous mats, which develop under a variety of hot spring flow conditions. Fly activity is generally restricted to cooler mats (from 30-35C), where most egg laying occurs. Above 40C the eggs fail to hatch and first instars die. At 35C the life cycle takes approximately 14 days (egg to egg), and mature females can produce 100 or more eggs a day. *Turbida* can exploit transient islands of available resource quickly, and the larvae soon decimate the optimum habitat (Weigert and Mitchell, 1973). Wiegert and Mitchell also analyzed the interactions between the algal mats and *turbida* and between *turbida* and a mite parasite *Partnuniella thermalis* Viets. Mitchell and Redmond (1974) describe the egg of *turbida* (several stereoscan electron micrographs) and suggest mechanisms of respiration under varying environmental conditions. *Paracoenia turbida*, however, is not endemic to hot springs, and the details of their feeding habits and habitat preferences under different conditions could vary considerably. More notes on the biology of this species may be found in Scheiring and Foote (1973).

Paracoenia (*Paracoenia*) *wirthi*, n. sp.

Fig. 6, Map 1

Diagnosis.— This species resembles both *P. bisetosa* and *P. turbida* and in many respects is intermediate. As in *P. bisetosa*, the ventral margin of the fifth abdominal tergite is produced into a pointed extension, but the projection is not as long as that of *P. bisetosa*. The general coloration and setal characters more resemble *P. turbida;* however, males of *P. wirthi* are destinct from either species in the shape of the surstyli, the hypandrial process, and the fifth abdominal sternite. Basally, the surstyli are wide, a condition that extends to about one-half their total length. The hypandrial process is broadly produced apically with a bluntly rounded apex. The fifth abdominal sternite is broad, and the projecting arms are subparallel and short.

Description.— Length 3.1-3.6 mm; subshinning with bluish-green to green metallic reflections.

Head. Mesofrons greenish-blue, shining; pruinose face grayish-tan; eye-to-cheek ratio 1:0.22; width-to-height ratio 1:0.6; height-to-length ratio 1:0.87; eye-width-to-face-length ratio 1:0.44.

Thorax. Acrostichal hairs in three to four rows anteriorly, becoming irregular with five to six rows posteriorly. Pleural areas although subdued not grayed. Wings in many specimens almost transparent, in others smoky infuscate.

Abdomen. Metallic reflections green to olive green. Male genitalia as in diagnosis and Fig. 6.

Distribution.— This species is found in the Sonoran desert from southern California and northern Baja California eastward into Arizona. It extends south into Mexico (Distrito Federal, Mixquic).

Types.— Male holotype, allotype and 21 paratypes (7 males, 14 females), California, Inyo Co., 1 mile N Tecopa Hot Springs, 24 June 1974, Wayne N. Mathis. Thirty-nine paratypes as follows: California, Inyo Co., Tecopa Hot Springs, 16 May 1965, W. F. Barr, 1 male; Inyo Co., Shoshone, 24 June 1974, W. N. Mathis, 1 male, 5 females; Inyo Co., Shoshone, 1 October 1935, A. J. Basinger, 1 male, 3 females; San Diego Co., Mtn. Palm Springs, Anza Desert, 2 March 1964, 1 male. Arizona, Pima Co., Lowell Ranger Station, 6-20 June 1916, 32°18.5′ N, 110° 49′ W, ca. 2,700′, 1 male, 1 female; Bill Williams Forest, August, F. H. Snow, 1 male, 1 female. Mexico, Baja California, Guadalupe Canyon, 19 May 1957, F. X. Williams, 1 male, 3 females; Distrito Federal, Mixquic, 9 km SW Chalco, 4 August 1965, K. R. Valley, 4 males, 16 females. The type, allotype, and 8 paratypes will be deposited in the California Academy of Sciences, type number 12033. The remaining paratypes will be deposited with the U. S. National Museum of Natural History, Cornell University, the Canadian National Collection, The Academy of Natural Sciences of Philadelphia, and my collection.

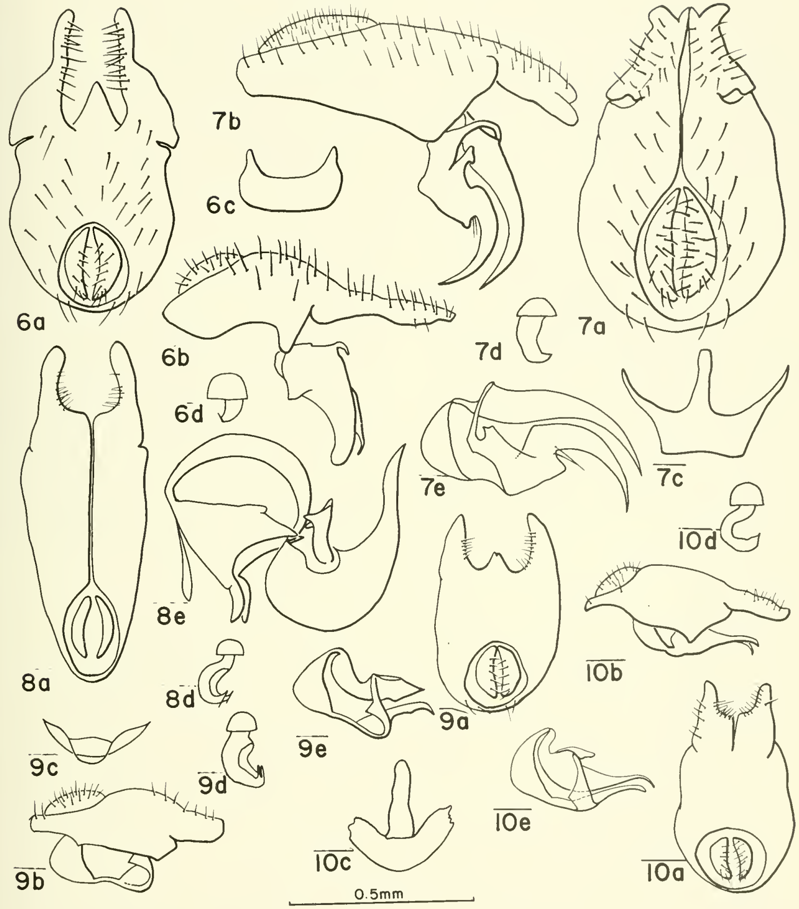
Remarks.— Although *P. wirthi* appears to be intermediate in many characters, their consistency, especially the male genitalia, justifies recognition as a new species. As with other species of the genus, *P. wirthi* is sometimes associated with hot springs, usually along the margins of the effluent.

P. wirthi is named to honor Dr. Willis W. Wirth for his contribution to the systematics of the Ephydridae and for his helpful, encouraging responses to my many questions.

Calocoenia, n. subgen.

Type-species: *Paracoenia platypelta* Cresson, 1935, monobasic

Diagnosis.— Although similar to *Paracoenia* s. str. and *Leptocoenia*, *Calocoenia*



Figs. 6-10.— Male and female genitalia. 6 a,b,c,d *Paracoenia wirthi;* 7 a,b,c,d,e *Paracoenia platypelta;* 8 a,d,e *Coenia curvicauda;* 9 a,b,c,d,e *Paracoenia paurosoma;* 10 a,b,c,d,e *Coenia alpina.* Fig. e, lateral view of internal genitalia; others as in caption of 1-5.

may be distinguished from either as follows: Externally, *Calocoenia* differs from *Paracoenia* s. str. in the arrangement of acrostichal hairs, which are in two distinct rows, by the absence of a posteroventral comb of bristles along the male mesofemora, by the flattened scutellum, by the prominent costal bristles projecting anteriorly from both dorsal and ventral margins, and by the generally uniform, concolorous abdomen which in male specimens is more noticeably narrowed apically. The most apparent difference between *Calocoenia* and *Leptocoenia* is size; *Calocoenia* is nearly twice the length of most *Leptocoenia.* Further, the eye-to-cheek ratio of *Calocoenia* is at least 1:0.2 and the M_{1+2} vein ratio is under 1:0.8. The male postabdomen is symmetrical; the epandrium is subelliptical with closely fused surstyli ventrally and with a median groove. The hypandrial process and aedeagus are tusklike, long, and well sclerotized. The aedeagal apodeme is crescent shaped.

Description.— Length 3.4–4 mm; subshining to shining, metallic brown to greenish-brown; pollinose, gray ventrally.

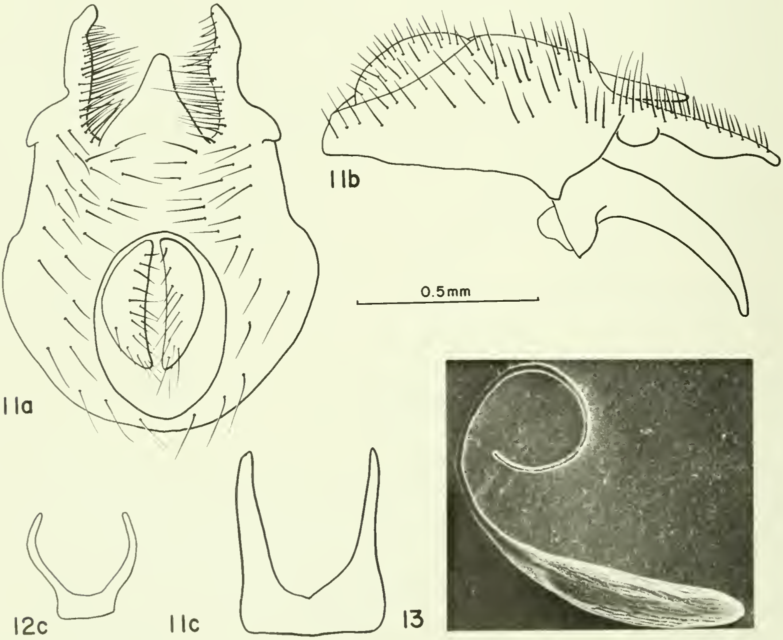
Head. Mesofrons shining, bronze-gold metallic reflections; pectinate branches of arista not more than twice aristal width at base; pruinose face tan; interfoveal hump not as prominent as *Paracoenia* s. str., dorsally sloping; eye large, subcircular, width in profile double the length of projecting face in profile; eye–to–cheek ratio 1:0.25; width–to–height ratio 1:0.66; height–to–length ratio 1:0.9. Chaetotaxy of head and thorax like *Paracoenia* s. str. except acrostichal hairs.

Thorax. Acrostichal hairs in two rows; dorsum pollinose to subshining; pleural areas concolorous with mesonotum centrally, becoming pollinose, grayed marginally; halters yellow. Male mesofemora without comb of bristles. Wings with costal bristles on dorsal and ventral margins; costal vein ratio 1:0.2.

Abdomen. Subshining to shining, brown metallic reflections; fifth abdominal tergite of male more or less truncate, without anteroventral process; fifth abdominal sternite with three posteriorily oriented prongs. Female postabdomen similar to *Paracoenia* s. str. Male postabdomen as in diagnosis, Fig. 7. Ventral receptacle with operculum wider than high, extending process considerably longer than operculum.

Discussion.— *Calocoenia* is a monotypic subgenus known only from the Nearctic Region. Nothing is known about the biology of the included species.

Although the type-species of *Calocoenia* was originally described in *Paracoenia* s. str., its inclusion with the latter subgenus would form a paraphyletic grouping since the sister group of *Calocoenia* is *Leptocoenia.* The sister-group relationship with *Leptocoenia* is deduced from the joint pos-



Figs. 11-13.— Male genitalia and egg. 11 a,b,c *Paracoenia beckeri;* 12c *Paracoenia fumosa;* 13 stereoscan electron micrograph of *Paracoenia calida* egg, 100 X. Figures as in caption of 1-5.

session of the following apomorphous features not found in *Paracoenia* s. str.: eye-to-cheek ratio less than 1:0.3; interfoveal hump not as pronounced as in *Paracoenia* s. str.; and the fifth abdominal tergite lacking an anteroventral process.

Paracoenia (*Calocoenia*) *platypelta* (Cresson)

Fig. 7, Map 1

Paracoenia platypelta Cresson, 1935, Trans. Amer. Ent. Soc. 61:356

Coenia (*Paracoenia*) *platypelta*: Sturtevant and Wheeler, 1954, Trans. Amer. Ent. Soc. 79:165

TYPES.— Male holotype, Pine Lake, So. Cal., Johnson. The type specimen also has a small label with the male sex symbol, Cresson's pink type label, and a red USNM type label, number 51110. The type is deposited with the U. S. National Museum of Natural History. Cresson's original description also lists a topotypical female paratype. I have examined this latter specimen, presently with the Academy of Natural Sciences of Philadelphia, and determined it as *Paracoenia turbida*.

DIAGNOSIS AND DESCRIPTION.— See generic description.

SPECIMENS EXAMINED.— 516

DISTRIBUTION.— This species is known only from the West (US). I have examined specimens from Washington to Alberta (Laggan) and southward to New Mexico, Arizona, and California. I have not seen specimens from Montana or Wyoming, although collection attempts have been made.

REMARKS.— *C. platypelta* is a very homogeneous species exhibiting little morphological variation. There is some color polymorphism, but this could represent age polymorphism. As mentioned previously, nothing is known regarding the biology or larvae of this species.

Leptocoenia, n. subgen.

TYPE-SPECIES.— *Coenia paurasoma* Sturtevant and Wheeler, monobasic

DIAGNOSIS.— *Leptocoenia* resembles *Calocoenia* but the body size is much smaller, length 2.1–2.6 mm, and the male postabdomen of *Leptocoenia* differs considerably. The surstyli are well separated apically with a small median triangular process between them, which is very similar to a comparable structure in *Paracoenia* s. str. The triangular process in *Paracoenia* s. str., however, is better developed in comparison with the lateral surstyli. Externally, *Leptocoenia* is similar to *Calocoenia*, and both share the following character states: The acrostichal hairs are in two distinct rows; the scutellum is slightly flat; the ventral margin of the fifth abdominal tergite is not produced into a lobe; and the posteroventral surface of the mesofemora does not bear a row of comblike bristles.

DESCRIPTION.— Length 2.1–2.6 mm; dark brown, pollinose.

Head. Fronto-orbital areas, mesofrons nearly concolorous, the later subshining; pectinate aristal branches at most two and one-half times aristal width at base; interfoveal hump not prominent, without pronounced dorsal indentation; pruinose face light tan; longest bristles along ventral margin of face approximately three-fourths length of interfoveal hump height; genal bristle weak, subequal to humeral bristles. Eye–to–cheek ratio 1:0.175; width–to–height ratio 1:0.65; height–to–length ratio 1:0.93; eye–width–to–face–length ratio 1:0.3.

Thorax. Lightly pollinose dorsally. Acrostichal setae in two rows; four pairs of dorsocentral bristles; humeral bristles present; halters yellowish-brown to brown. Costal setae weak, developed only on dorsal margin.

Abdomen. Male postabdomen as in Fig. 9; ventral receptacle as in Fig. 9d.

DISCUSSION.— In many respects, this subgenus is pivotal, linking *Paracoenia* with *Coenia*. This is evident in characters associated with size and dimension, but the annectant role of *Leptocoenia* is best evidenced by the shape of the female ventral receptacle. The ventral receptacle closely resembles those of *Coenia* species and is probably less likely to be affected by selective pressure, which would bring about convergence in dimension and size of external characters except by pleiotrophy. I attribute considerable importance to this feature and the relationship with *Coenia* that it demonstrates.

The internal male genitalia of *Leptocoenia* also reflect the intermediate position of this subgenus with *Coenia*. This is best seen by comparing Figs. 9e and 10e.

Paracoenia (*Leptocoenia*) *paurosoma* (Sturtevant and Wheeler)

Fig. 9, Map 3

Coenia paurosoma Sturtevant and Wheeler, 1954, Trans. Amer. Ent. Soc. 79:165

Paracoenia paurosoma: Wirth, 1965, USDA Agri. Handbook No. 276, p. 567

Types.— Female holotype, three paratypes (one male, two females), Lander, Wyoming, 16 August 1950. The holotype also bears a collector label, M. R. Wheeler, and type number 6696. A fourth paratype (female), Rainbow Lake, Colorado, elev. 10,200′, 50 hl. The original description indicates that K. W. Cooper was the collector of the fourth paratype, but no collector label accompanied the specimen. The holotype is deposited with the Academy of Natural Sciences of Philadelphia, two paratypes with the U.S. National Museum of Natural History, and two paratypes with M. R. Wheeler.

Diagnosis and Description.— See generic description.

Specimens examined.— 41

Distribution.— *Paurosoma* has been collected from Colorado north through Wyoming, Alberta (Laggan), and into Alaska (Matanuska Flats). I have also examined five specimens from Sweden (Norrbotten, 3 km N Messaure).

Although *paurosoma* is Holarctic, it was the most recently discovered species. Moreover, nothing is known about its biology. The habitat of this species is montane; at lower latitudes it is found at elevations up to 10,500 feet (Rainbow Lake, Colorado).

Genus *Coenia* Robineau-Desvoidy

Coenia Robineau-Desvoidy, 1830, Essai sur les Myodaires 2:800. Type-species *Coenia caricicola* Robineau-Desvoidy (= *Ephydra palustris* Fallén), by monotypy; Sturtevant and Wheeler, 1954. Trans. Amer. Ent. Soc. 79:164-166 (review of Nearctic species as subgenus of *Coenia*); Wirth, 1965, USDA Agri. Handbook No. 276, pp. 755-756 (catalog)

Caenia emendation: Walker, 1853, Insecta Britannica Diptera 3:259 (preoccupied-Newman, 1853, Entomological notes. Art X. Ent. mag., pp. 372-402, Coleoptera)

Diagnosis.— *Coenia* species resemble those of *Paracoenia*, especially the subgenus *Leptocoenia*, but they are differentiated as follows: Dorsalmost postocular bristles not subequal to the verticals; no well-developed humeral bristles; two pairs of dorsocentral bristles; halters brownish-yellow to dark brown; and fifth abdominal sternite of males longer than wide. The size of *Leptocoenia* is within the dimensions of *Coenia*, and superficially they appear very similar. However, the chaetotaxy characters readily distinguish either and set the *Coenia* species apart from any *Paracoenia* subgenus.

Description.— Length 2.2-2.8 mm; dark brown, pollinose to subshining.

Head. Mesofrons subshining with metallic reflections; postocular bristles weak, at most slightly larger than their distance apart as base; postorbital bristles usually weak; pectinate aristal branches various; bristles of face comparatively large, bristles along ventral margin subequal in length to interfoveal hump height; facial pruinosity various; chaetotaxy of head similar to *Paracoenia* except as noted. Eye relatively large, subcircular although higher than wide; width–to–height ratio 1:0.62; height–to–length ratio 1:0.95; eye-width–to–face–length ratio 1:0.3.

Thorax. Dark brown, generally concolorous; strength of pollinose covering various. Acrostichal hairs in two rows, indistinct in some species. Three or four pairs of dorsocentral bristles; humeral bristles various; otherwise chaetotaxy as in *Paracoenia.* Wings without prominent costal bristles, at most weakly developed on dorsal margin; costal vein ratio 1:0.3; M_{1+2} vein ratio 1:0.7. Legs uniformly dark brown; male mesofemora without posteroventral comb. Halters as in diagnosis.

Abdomen. Subshining to shining dark brown; male with five visible tergites; female with six to seven; male with five sternites; fifth sternite narrowed to small strip; spiracle arrangement as in *Paracoenia.* Male postabdomen with surstyli closely apposed basally, becoming well separated on apical 2/3; aedeagal apodeme broad to narrowly crescent-shaped; aedeagus curved, pointed apically. Ventral receptacle with small operculum, extending process C-shaped.

Discussion.— Of the three known *Coenia* species, one is apparently endemic to the Nearctic Region, a second is limited to the Palearctic, and a third species is Holarctic. Cresson's comments regarding the European species and their distinguishing characteristics should be consulted for species separation from that fauna.

Species of *Coenia* are not usually associated with aquatic environments that are contaminated or contain high concentrations of various salts. Dahl (1959) and Scheiring and Foote (1973) report on associations of *Coenia curvicauda* (Meigen) with mud shore habitats and to a lesser extent with the limnic wrack.

Key to *Coenia* species

1. Male genitalia large, exposed ventrally; epandrium over twice as long as wide, with median suture .... *C. curvicauda* (Meigen)
   Male genitalia more compact, not exposed; epandrium less than twice as long as wide, without median suture .... *C. alpina* n. sp.

Coenia alpina, n. sp.

Fig. 10, Map 2

Diagnosis.— *C. alpina* most closely resembles *C. palustris*, a Palearctic species. It is distinguished from the latter by differences in male genitalic structures. The surstyli are proportionately shorter to the epandrial length, the aedeagus is deeper and ventrally rounded, the aedeagal apodeme is longer, and the hypandrial processes are thinner and project mesad to the hypandrial connection with the aedeagus. The females of both species are very similar.

Description.— Length 2.1–2.6 mm; dark brown with some purplish metallic reflections dorsally.

Head. Interfoveal hump more or less prominent; pruinose face brown; pectinate branches of arista long, approximately three times aristal width at base; postorbital setae not developed dorsally. Eye-to-cheek ratio 1:0.12; width-to-height ratio 1:0.6; height-to-length ratio 1:0.96; eye-width-to-face-length ratio 1:0.33.

Thorax. Acrostichal setae weak, in two rows; three pairs of dorsocentral bristles; humeral bristles absent; halters dark brown.

Abdomen. Subshining to shining with some purplish reflections; ventral receptacle as in Fig. 10d; male genitalia as in Fig. 10.

Distribution.— *C. alpina* has been collected in Colorado (Rabbit Ears Pass), in the Northwest Territories (Aklavik), and in Labrador (Cartwright).

Types.— Male holotype, allotype, and 21 paratypes (8 males, 13 females), Cartwright, Labrador, 29 June 1955, E. F. Cashman; 17 paratypes with same data as type except as follows: 5 males, 3 females, 3 July 1955; 4 males, 2 females, 2 July 1955, E. E. Sterns; 1 male, 6 August 1955, E. E. Sterns; 1 male, 12 August 1955. The type, allotype, and 32 paratypes will be deposited with the Canadian National Collection, type number 13435. A male and female paratype also will be deposited with the California Academy of Sciences, the U.S. National Museum of Natural History, and in my collection.

In addition to the type series, I have examined 31 specimens of this species from the following localities: 9 males, 17 females, Aklavik, Northwest Territories, May-August 1930 and 1931; 2 males, 3 females, Rabbit Ears Pass, Colorado, 11 June 1968, S. L. W.

Remarks.— This species is alpine, which accounts for the specific name. Although the known distribution is based on minimal data that is rather disjunct, I feel that *C. alpina* is distributed throughout the Rocky Mountains at higher elevations and across northern Canada.

From my study, I have found very little variation except for minor size differences as indicated in the description. Otherwise, *C. alpina* seems to be a very uniform species.

Coenia curvicauda (Meigen)

Fig. 8, Map 3

Ephydra curvicauda Meigen, 1830, Syst. Beschr. 6:116

Coenia curvicauda: Macquart, 1835, Hist. Nat. Ins. Dipt. 2:530

Types.— Cresson (1930) designated a lectotype for this species from material in the Naturhistorisches Museum, Wien. According to Cresson, the male lectotype has the following label data: "curvicauda Coll. Winth," "curvicauda." A second male specimen with similar data was designated a paratype by Cresson.

Diagnosis.— *C. curvicauda* is similar to *C. alpina* and to *C. palustris* but differs from either by the well-developed male postabdomen which protrudes from the venter of the abdomen. The epandrium plus surstyli are over twice as long as the epandrial width, and the epandrium is divided by a median groove. The surstyli arms are longer than their base, the aedeagal apodeme is slender and C-shaped in profile, and the aedeagus is broadly developed basally and curves forming a J-shaped structure.

Description.— Length 2.3–2.8 mm; dark brown, subshining to shining.

Head. Mesofrons shining, dark brown; fronto-orbital areas subshining; pectinate aristal branches subequal to third antennal segment width; face lightly pollinose, mostly dark brown; chaetotaxy as in *C. alpina;* eye-to-cheek ratio 1:0.11; width-to-height ratio 1:0.6; height-to-length ratio 1:1; eye-width-to-face-length 1:0.3.

Thorax and abdomen as in *C. alpina* except as given in diagnosis.

Specimens examined.— 150

Distribution.— *Coenia curvicauda* is a Holarctic, boreal species. In the Nearctic region it is found in Montana (Bigfork) and east through the Midwest to the Northeast. It extends north to Alaska (Tonsina) and east to Quebec (Cross Point).

Remarks.— Although I did not examine the lectotype, I have studied European specimens of this species. The aedeagus in some specimens does not curve apically to the extent found in Nearctic specimens, but I did not find any other major differences. I consider all specimens I examined to be conspecific.

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ENVIRONMENTAL FACTORS IN RELATION TO THE SALT CONTENT OF *SALICORNIA PACIFICA* VAR. *UTAHENSIS*[1]

D. J. Hansen[2] and D. J. Weber[2]

Abstract.— The stability of the salt content in *Salicornia pacifica* Standl. var. *utahensis* (Tidestrom) Munz in relation to environmental changes was investigated. *Salicornia pacifica* communities have a characteristic soil pH of 7.5 to 8.0 ± 0.2 and a constant subsurface soil moisture level of 25 to 35 percent. The ion content in the tissue of *S. pacifica* remained constant despite increased moisture stress throughout the growing season. The concentrations of the salts were significantly higher in the surface soil layers than in the subsurface layers around the roots. Normal metabolic processes in the tissues of *S. pacifica* appear to occur even though some fluctuations in the ionic balance and concentration of ions in the plant occur.

Introduction

Halophytic plants are among the few species of higher plants that can withstand high saline soil conditions without detrimental effects (Waisel, 1972). The is mainly associated with an increase in the chloride content of the tissues (Adriani, 1958; Bernstein, 1961). Steiner (1935) found that chloride ions accounted for 67 to 88 percent of the increase of osmotic potential of different species of salt marsh plants, whereas other osmotically active substances had only a negligible effect. Chloride accounted for 80 percent of the total osmotic potential in *Salicornia ambigua*, 91 percent in *S. stricta*, and 93 percent in *S. mucronata* (Arnold, 1955). Harward and McNulty (1965), on the other hand, found that chloride accounted for less than 49 percent of the osmotic potential in *S. rubra*.

Osmotic values for leaf saps of a number of herbaceous halophytes including *S. herbacea*, ranged from 25 to 75 atm when grown in salt marshes (Yabe et al., 1956). Seasonal changes in osmotic potentials in tissues of *S. rubra* ranged from 40 atm to over 100 atm over a two-month period (Harward and McNulty, 1965). Higher osmotic potential values have been recorded for a number of halophytes; for example, Waisel (1972) reported that osmotic potentials of *Rhizophora* and *Avicennia* leaves reached values of 148 and 163 atm, respectively.

According to Bowen and Rovira (1966), salt ions can cause toxicity in the following ways: (1) acting as antimetabolites, (2) binding or precipitating various metabolites, (3) catalyzing rapid decomposition of essential elements, (4) combining with cell membranes and affecting their permeability, and (5) displacing essential elements but failing to fulfill their functions. Bowen and Rovira (1966) suggested that salt injury is not due to a direct effect of the salts but to the indirect effects of one or more of the above mentioned metabolic disturbances. Waisel (1972) singled out nitrogen metabolism as an important area affected by high salts. Salt-induced growth retardation leads to an accumulation of unused substances that may be toxic (Gauch and Eaton, 1942).

The degree of salt injury or tolerance of plants may be affected by a number of environmental factors such as waterlogged soils. Some plants, however, have adapted to waterlogged conditions. *Salicornia foliosa* not only tolerates waterlogged conditions but appears to benefit from them, because of increased capacity to obtain iron under these conditions thereby avoiding chlorosis (Adams, 1963). In habitats with marked fluctuations in salt concentration, only the species with high osmotic shock resistance (*Salicornia sp.*) can survive (Levitt, 1972). Some of the facultative halophytes, such as *Salicornia rubra*, are found at the highest salinities yet are capable of growing normally in low to nonsaline environments (Ungar et al., 1969).

Since species of *Salicornia* are among the most salt tolerant forms of higher plants (Chapman, 1960), *S. pacifica* Standl. var. *utahensis* (Tidestrom) Munz., a halophyte common to inland salt playas of northern Utah, was selected for this investigation. Due to the lack of basic information about environmental fluctua-

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[1] This research was supported in part by NSF Grant No. GB31067 and a research grant from Brigham Young University.

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tions in *S. pacifica* habitats and difficulties in providing an artificial environment that parallels the natural environment, investigations were undertaken to correlate fluctuations of the natural environment with physiological and morphological characteristics in relation to salt content of *S. pacifica.*

Methods and Materials

This investigation was conducted during a typical growing season for *Salicornia pacifica* (April to August 1972). Three sites were selected to compare soil and moisture factors in relation to changes in salt content of *S. pacifica.* Sites 1 and 2 were six miles (9 km) north and Site 3 was about one-half mile (1 km) east of Goshen, Utah. Site 1 was especially selected because it was an ecotone between a stand of *S. pacifica* and a stand of *Distichlis stricta.* It was hoped that the data from this site could be used to explain some of the environmental factors responsible for separating the *Salicornia* communities from the *Distichlis* communities.

The ground at Site 1 was covered by a thin layer of dried algae of the genus, *Oscillatoria.* This covering formed a surface mulch which increased the moisture of the soil surface. Site 2 was about 100 m west of Site 1 on the opposite side of a large drainage basin. Site 3 (Fig. 1) was 6 miles (9 km) from Sites 1 and 2 adjacent to a natural drainage system. Site 3 was selected because of reduced fluctuations in soil moisture throughout the growing season. Soil and plant samples were taken every two weeks at all three sites.

A standardized hygrothermograph unit was used to continuously monitor temperature and relative humidity. The housing unit for the hygrothermograph was located three inches above the ground about 100 m from Sites 1 and 2. Measurements were recorded from 1 May through 20 September 1972.

The percentage of plant cover for Sites 1, 2, and 3 was determined using eight randomly distributed rectangular ¼ m^2 quadrats. Dry weight production in each site was determined by clipping four randomly distributed rectangular ¼ m^2 quadrats.

Soil samples were taken with a soil core borer. Each core measured 1 inch (2:54 cm) in diameter and was extended to a depth of 10 inches (25.4 cm). The cores were separated to provide surface (upper

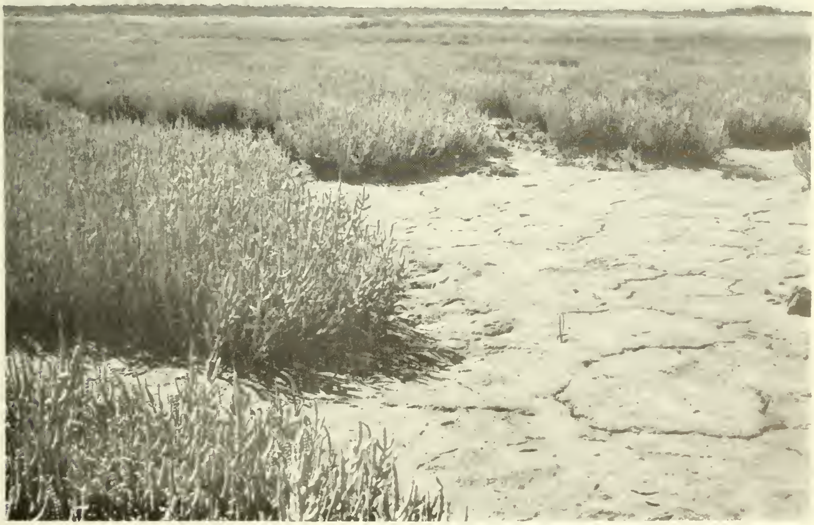

Fig. 1. Site 3, located one mile east of Goshen, Utah, showing a typical stand of *Salicornia pacifica* (Photograph courtesy of W. M. Hess.)

2 inches or 5 cm of the core) and subsurface (lower 6-10 inches or 15-25 cm of the core) soil samples. Five to eight core samples were taken at each site and pooled to obtain the soil sample. The samples were placed in plastic bags, sealed, and immediately taken to the laboratory for analysis. Samples were weighed to the nearest one-hundredth of a gram and dried in an oven at 110C for 48 hours. The samples were weighed again, and the percentage of moisture was calculated.

Measurements of the soil pH were determined from saturated soil paste samples using the Sargent-Welch pH Meter, Model PAX, with a combination electrode.

Osmotic potentials of soil samples were determined from saturated soil pastes by freezing-point depression methods according to the procedure outlined by Hansen and Weber (1974).

Soil samples (5 g) were leached of exchangeable cations and anions by flushing with four 25 ml volumes of 1N $CH_3\text{-}\overset{O}{\overset{\|}{C}}\text{-}NH_2$, pH 7.0. Each volume was allowed to drain before the next was applied. The cations (sodium, potassium, magnesium, and calcium) were detected in the filtrate according to procedures outlined by Perkin-Elmer (1971) on the Model 290B Atomic Absorption Spectrophotometer. The anion, chloride, was detected in the filtrate according to the procedure outlined by Marius/Fiske (1972) using a Marius/Fiske Chlor-o-counter.

Osmotic potential measurements for *Salicornia* were determined by freezing-point depression techniques as described by Cary and Fisher (1969, 1971) and Fisher (1972). The circuitry was modified by replacing the two 1.35 vdc Hg battery cells with an alkaline 9 vdc battery. A 10K 1-turn potentiometer was installed to compensate for voltage drop that occurred with time and usage. Measurements were made at each internode for several plants. Measurements were occasionally made using a vapor pressure osmometer, Model 301 Mechrolab Inc., to verify freezing-point measurement values.

The percentage of crude protein in each plant sample was determined by the micro-Kjeldahl method (Horwitz, 1970).

TABLE 1. Percentage moisture, dry weight production, and percentage cover of *Salicornia pacifica* in three salt desert playas.

Site	Percentage moisture	Dry weight production g/m²	Percentage cover
1	79.0	73.1	56.0 *S. pacifica* 2.5 *S. rubra*
2	80.6	26.7	7.5 *S. pacifica* 1.0 *A. occidentalis*
3	80.6	141.2	65.0 *S. pacifica* 2.5 *S. rubra*

Results

Climatic and Growth Factors

Continuous hygrothermograph monitoring of climatic factors indicated that temperatures fluctuated consistently throughout the growing season. The average temperatures gradually increased through May and June. A peak was reached during July, followed by a gradual decrease from August to September. The average of the daily highs during July was 34C. The hottest temperature in July was 38C on 12 July. The coolest temperature recorded in July was 6C on 25 July.

Lowest daily means (calculated on an hourly basis) for relative humidity occurred from 15 July through 20 August. A series of rain storms increased the relative humidity during late August and early September. Light rain was also common during late May and early June. No quantitative data concerning the amount of rain was taken. Relative humidity reached 100 percent every night except for about six days during the growing season.

The dry weight of the standing crop of *S. pacifica* plant tissue was the highest on Site 3 (141.2 g/m²) and the lowest on Site 2 (26.7 g/m²) as shown in Table 1. The percentage cover was also highest on Site 3 (65 percent) and lowest on Site 2 (7.5 percent). The percentage moisture of the plants in all three sites was about 80 percent.

Soil Moisture

The subsurface and surface soil moisture readings for Site 2 were highest during June, gradually decreasing throughout the growing season (Fig. 2). The subsurface soil moisture for this site was less than the surface soil moisture from 1 April through 15 July. This may have been due to the heavy mulch of algae on the surface. However, from mid-July through the rest of the season, this trend

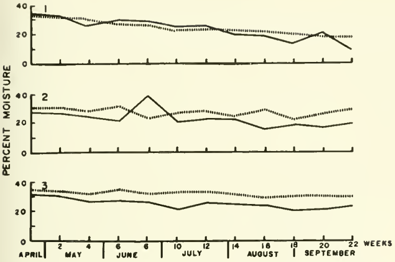

Fig. 2. Soil moisture for three salt desert playas (Sites 1, 2, and 3). Solid lines indicate the plot of percentage values for surface soil samples (upper 2"). Dashed lines indicate the plot of percentage values for subsurface soil samples (6-10").

was reversed. In Sites 2 and 3 the subsurface soil moisture was consistently higher than the surface soil moisture throughout the growing season, except for one week in June when Site 2 had an increase in the surface soil moisture due to rainfall. Surface and subsurface soil moisture percentages at Site 3 were well above moisture percentages of Sites 1 and 2. From June through July soil moisture in Site 3 was above 30 percent, whereas soil moisture of Sites 1 and 2 was well below 30 percent. This was probably due to underground seepage from the nearby drainage system adjacent to Site 3. Soil moisture was lowest in all three sites during May.

Soil pH

The surface soil pH of the three sites was generally higher and fluctuated more than the corresponding subsurface pH (Fig. 3). The subsurface pH of these sites changed very little during the growing season. The decrease in the pH of the soil surface appeared to be correlated to the amount of rainfall. This effect was probably due to the transporting of soluble salts into the subsurface layers by the percolating rain. A decrease in the pH of the surface generally was inversely proportional to the increase in the subsurface pH.

Ion Content of the Soil

Site 1

Osmotic potential measurements of the surface soil were high during July and September. Osmotic potential values were

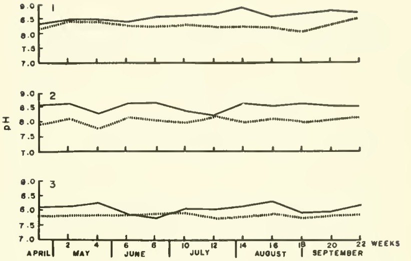

Fig. 3. Soil pH as recorded for three salt desert playas (Sites 1, 2, and 3). The solid lines indicate the plot of the pH for surface samples (upper 2"). The dashed lines indicate the plot of the pH for subsurface samples (6-10").

as high as 135 atm (Fig. 4). Osmotic potential measurements of subsurface soil samples were considerably lower than osmotic potential measurements of the surface. Osmotic potential values for the subsurface soil samples gradually increased. The highest value reached was 48 atm. This value was recorded on 20 September, when the study terminated. Values during the hottest month did not exceed 23 atm.

Individual ion analysis of soil samples from the surface (Fig. 5) and the subsurface layers (Fig. 6) showed that sodium and chloride were the two ions responsible for most of the osmotic potential. The increasing ion accumulation of the soil closely paralleled the increase in osmotic potential previously described. The con-

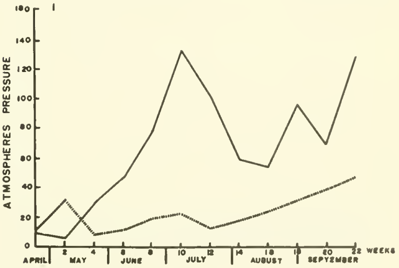

Fig. 4. Osmotic potential of saturated soil paste for a salt desert playa (Site 1) expressed as atmospheres pressure. The solid line indicates the plot of osmotic potential values for the surface soil samples (upper 2"). The dashed line indicates the plot of osmotic potential values for the subsurface samples (6-10").

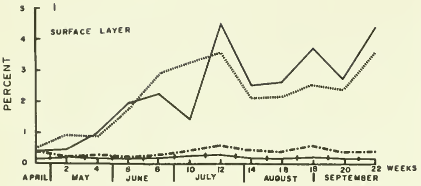

Fig. 5. Ion content of the soil for the surface layer (upper 2") of a desert playa (Site 1) expressed as a percentage of the dry soil. The solid line indicates the percentage of chloride. The dashed line indicates the percentage of sodium. The dash-dotted line indicates the percentage of calcium. The solid vertical-barred line indicates the percentage of potassium.

centrations of sodium and chloride were highest during July and September. The concentration levels of calcium and potassium ions were fairly constant throughout the season. Concentration values seldom exceeded 0.5 percent of the dry soil weight in either the surface or the subsurface layers.

Site 2

Osmotic potential values for the surface layer samples were uniform and high (over 130 atm) throughout the season with the exception of a substantial decrease on 29 August, when values dropped to 80 atm (Fig. 7). The subsurface values steadily increased throughout the growing season to a high of about 96 atm on 20 September. In most cases osmotic potential values of the subsurface soil samples were 50 to 100 atm lower than osmotic potential values of the surface soil samples. Thus, roots near the surface would be in an environment of higher moisture stress than deeper roots.

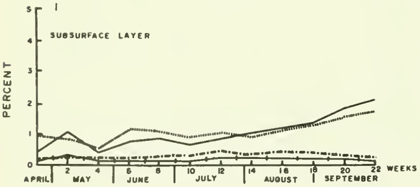

Fig. 6. Ion content of the soil for the subsurface layer (6-10") of a salt desert playa (Site 1) expressed as a percentage of the dry soil. The solid line indicates the percentage of chloride. The dashed line indicates the percentage of sodium. The dash-dotted line indicates the percentage of calcium. The solid vertical-barred line indicates the percentage of potassium.

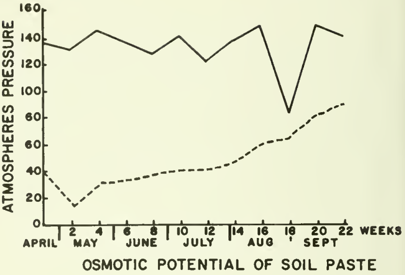

Fig. 7. Osmotic potential of saturated soil paste for a salt desert playa (Site 2) expressed as atmospheres pressure. The solid line indicates the plot of osmotic potential values for the surface soil samples (upper 2"). The dashed line indicates the plot of osmotic potential values for the subsurface soil samples (6-10").

Ion analysis of the surface layer soil samples showed that sodium and chloride ions were responsible for most of the osmotic potential of the soil samples (Fig. 8). The calcium ion concentration of the surface layer for this site was considerably higher than for Site 1. The subsurface calcium and potassium ion concentrations were comparable with other sites and rarely exceeded 0.5 percent of the soil dry weight (Fig. 9). The combined ion concentration in the subsurface layer increased gradually over the growing season and reached a peak of about 6 percent soluble salts on 20 September.

Site 3

Osmotic potential measurements of soil samples on this site gradually increased in both the surface and subsurface layers. Measurements were highest on 20 July and 20 September (Fig. 10) and were comparable with measurements from Site 2, both of which were considerably higher than Site 1.

Chloride ion content from the surface layer fluctuated considerably, but the sodium content was more stable (Fig. 11). The major increase in osmotic potential of the subsurface layer from 20 July through 20 September was due chiefly to the chloride ion content. The calcium ion concentration level of this site was considerably higher than Site 1 and not as high as Site 2. The potassium ion concentration level was less than 0.5 percent

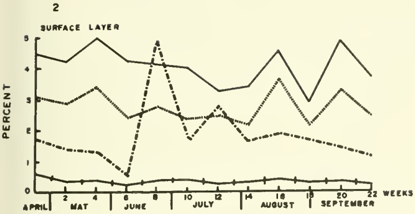

Fig. 8. Ion content of the soil for the surface layer (upper 2") of a salt desert playa (Site 2) expressed as a percentage of the dry soil. The solid line indicates the percentage of chloride. The dashed line indicates the percentage of sodium. The dash-dotted line indicates the percentage of calcium. The solid vertical-barred line indicates the percentage of potassium.

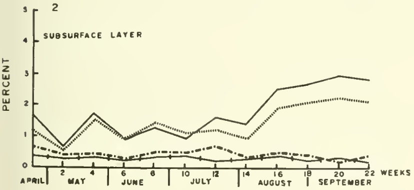

Fig. 9. Ion content of the soil for the subsurface layer (6-10") of a salt desert playa (Site 2) expressed as a percentage of the dry soil. The solid line indicates the percentage of chloride. Th dashed line indicates the percentage of sodium. The dash-dotted line indicates the percentage of calcium. The solid vertical-barred line indicates the percentage of potassium.

and did not fluctuate significantly. The concentration level gradually increased to a peak of 0.5 percent on 20 July and then gradually decreased to 0.3 percent on 20 September. Concentrations of sodium and chloride ions in the subsurface soil samples gradually increased (Fig. 12). Calcium and potassium ion concentrations in this layer remained low and relatively constant through the growing season; these ion concentrations were comparable to ion concentrations of the other sites.

Ion Content in Salicornia

Site 1

The chloride ion content in *Salicornia* tissues remained constant throughout most of the growing season but increased slightly in April (Fig. 13). This increase was followed by a stabilization of the concentration at about 12 percent of the dry weight. Sodium ion concentration gradually increased from about 4.2 to 9 percent, while potassium ion concentration decreased throughout the season from 2.2 to 1 percent.

Site 2

The chloride content gradually increased from 14.2 to 16.1 percent at the end of the growing season (Fig. 14). Increase in the sodium content was proportional to the increase in the chloride content and was 10.2 percent at the end of the growing season. The potassium ion concentration increased from 4.5 to 7.5 percent and was closely correlated to decreases in the sodium ion concentration.

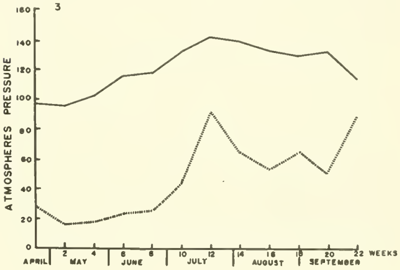

Fig. 10. Osmotic potential of saturated soil paste for a salt desert playa (Site 3) expressed as atmospheres pressure. The solid line indicates the plot of osmotic potential values for the surface soil samples (upper 2"). The dashed line indicates the plot of osmotic potential values for the subsurface samples (6-10").

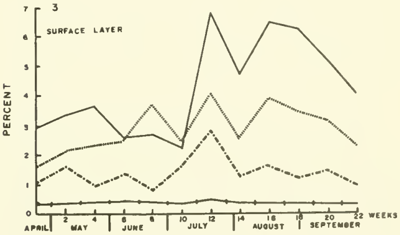

Fig. 11. Ion content of the soil for the surface layer (upper 2") of a salt desert playa (Site 3) expressed as a percentage of the dry soil. The solid line indicates the percentage of chloride. The dashed line indicates the percentage of sodium. The dash-dotted line indicates the percentage of calcium. The solid vertical-barred line indicates the percentage of potassium.

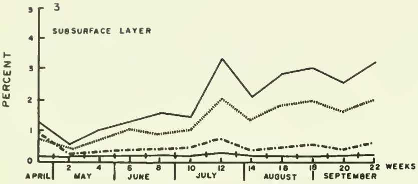

Fig. 12. Ion content of the soil for the subsurface layer of a salt desert playa (Site 3) expressed as a percentage of the dry soil. The solid line indicates the percentage of chloride. The dashed line indicates the percentage of sodium. The dash-dotted line indicates the percentage of calcium. The solid vertical-barred line indicates the percentage potassium.

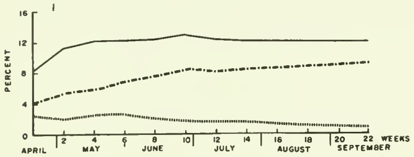

Fig. 13. Ion content in *Salicornia pacifica* (Site 1) expressed as a percentage of the dry weight. The solid line indicates the plot of the percentage values for chloride ions. The dash-dotted line indicates the plot of the percentage values for sodium ions. The dashed line indicates the plot of the percentage values for potassium ions.

Site 3

The ion content in *Salicornia* tissues in this site showed a decrease in chloride, sodium, and potassium throughout the season (Fig. 15). The chloride content ranged from 16 percent on 1 May to 12.4 percent on 20 September. The sodium content ranged from 11 percent on 1 May to 7.6 percent or 20 September. The potassium content ranged from 4.8 percent on 1 May to 2.1 percent on 20 September.

Osmotic Potentials in Salicornia

Early in the investigation it was discovered that each internode of the plant was osmotically different from other internodes of the same plant. Freezing-point depression measurements showed that osmotic potential values increased from the base of the aerial shoot upward to the top of the plant (Table 2). The lowest internodes near the base generally had a lower osmotic potential than internodes near the middle of the plant. In some cases there was as much as 15 atm difference between two regions (inner and outer) of the cortex, although usually the difference was only about 5 atm (Table 2). Because of the complexity of such differences in osmotic potential readings, only periodic measurements were made on the plants. The measurements ranged from a low of about 80 atm in May to about 130 atm to 150 atm in mid-July and August. However, the average was about 90 to 100 atm.

Crude Protein Analysis

Crude protein analysis showed a gradual decrease in the total crude protein content in the plants from all three sites from 1 April through 30 July. Crude protein decreased from 20 to 8 percent on a dry weight basis. From 30 July through 20 September the content remained about 8 percent.

Phenology and Morphology

Growth of *S. pacifica* usually begins with development of the subterranean or

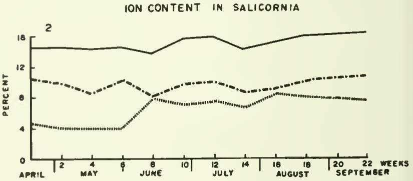

Fig. 14. Ion content in *Salicornia pacifica* (Site 2) expressed as a percentage of the dry weight. The solid line indicates the plot of the percentage values for chloride ions. The dash-dotted line indicates the plot of the percentage values for sodium ions. The dashed line indicates the plot of the percentage values for potassium ions.

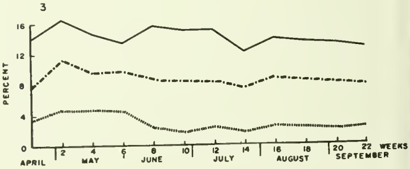

Fig. 15. Ion content in *Salicornia pacifica* (Site 3) expressed as a percentage of the dry weight. The solid line indicates the plot of the percentage values for chloride ions. The dash-dotted line indicates the plot of the percentage values for sodium ions. The dashed line indicates the plot of the percentage values for potassium ions.

TABLE 2. Osmotic potentials of four different *S. pacifica* plants showing the values (atm) of the outer and inner "cortex" tissues from the bottom of the shoot (Node 1) to the top of the shoot (Node 5).

Node	Plant A Inner	Plant A Outer	Plant B Inner	Plant B Outer	Plant C Inner	Plant C Outer	Plant D Inner	Plant D Outer
1	76	76	81	81	73	73	84	89
2	69	89	57	75	61	80	64	74
3	71	86	93	86	83	96	71	74
4	67	67	96	106	68	83	73	79
5	106	130	96	106	103	108	84	88
6	89	92	----	----	93	108	----	----
7	106	112	----	----	----	----	----	----

near-subterranean axillary buds of older shoots that start to grow in March and emerge in late April or early May. Flowering occurs in mid-June and is generally completed in July.

By late August lower internodes begin to wither and die sequentially from the base of the shoot to the tip (Fig. 16). Occasionally internodes may become injured or for other reasons may wither and die. The central stele continues to function in a normal manner. Seed-producing internodes are the last to die (Fig. 16). It is not known whether the internodes die strictly by senescence, whether accumulation of additional salts in these areas causes death, or whether death is related to some other phenomenon.

The seeds are shed in October and November. A few seeds adhere to the mother plant until rain or heavy snows separate them. Seeds are protected by a bulky, lightweight seed coat that aids in dispersal and absorption of moisture.

Seasonal Variations of the Environment

Temperatures were highest during July, while relative humidity was lowest during July and August. These high temperatures would cause increased moisture stress.

The toxicity of salts increases with the temperature, according to Kaho (1926) and Waisel (1972). The high moisture content of the soil and the subsequent evaporation may have had a cooling effect upon the temperature of the soil. Both lower temperatures and high relative humidity would have a favorable effect upon plant survival.

At all three sites there was an increase in moisture stress throughout the season primarily due to increases in salt from underground sources and slight decreases in soil moisture. Soil moisture of 25 to 35 percent is perhaps an important factor in maintaining *S. pacifica* in the environment.

Sodium and chloride were the two principal ions responsible for increases in osmotic potential of soil samples. They were also responsible for 85 to 95 percent of the osmotic potential of *S. pacifica*. Harris (1915) considered NaCl the most toxic of several soluble salts but concluded that salt mixtures were not as toxic in soils as in culture solutions.

The salt concentration of the soil surface layers was considerably higher than the salt concentration in the rooting layers. Soil surface layers were often encrusted with deposits of white salt, which gave the impression that the plants were surrounded by extremely high concentrations of salt when, in fact, the rooting zones or layers were only moderately saline. This observation was also reported by Wiesel (1972). The wicking action caused by evaporation of water resulted in salt crystallization at the surface, which removed salts from the rooting layers and provided a unique environmental niche for *S. pacifica* to occupy. Succulents such as *Salicornia* appear to lose the function of portions of their fleshy cortex and leaves (Fig. 16), yet the vascular system continues to function for the upper fleshy tissue (Fig. 16). The thick cuticle and waxy layer of the plants and the active phellogen of the central stele appear to protect the upper shoots from the more severe environmental stresses.

The soil pH was relatively stable throughout the growing season in all three sites. The surface soil pH of each site was about one-half pH unit higher than the subsurface pH. Decreases in the pH of the surface layers were proportional to increases in pH of the subsurface layer. Conversely, increases in the pH on the surface layer were proportional to de-

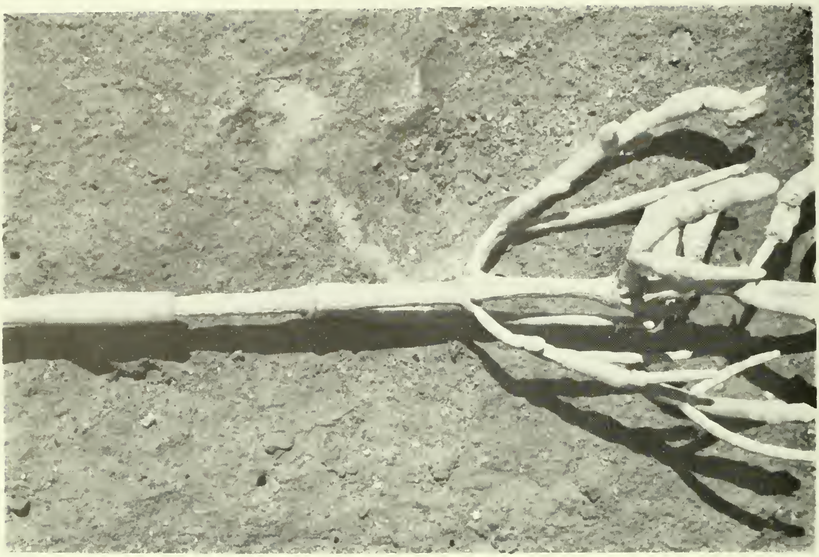

Fig. 16. Shoots of *Salicornia pacifica* showing healthy fleshy portions of stem above dead fleshy sections of cortex.

creases in the pH of the subsurface layer. Calcium ion concentrations in the surface layers were considerably higher at Sites 2 and 3 than at Site 1. Soil pH at Sites 2 and 3 was significantly lower than at Site 1. The pH may have been indirectly affected by the calcium concentration or may have been related to the algal covering of the soil surface in Site 1.

Ecological Interactions and Plant Distribution

There appear to be two groups of thought explaining the restriction of *Salicornia* to a saline environment. Newwohner (1938) stated that halophytes fail to succeed in fresh-water habitats because of competition with other species. This idea was supported by Stalter and Batson (1969), who stated that survival and growth rate data of transplanted salt marsh vegetation suggest that several species of halophytes (*S. virginica* included) can tolerate conditions not found in their usual zones. Montfort *et al.* (1927), on the other hand, claimed that this explanation of plant distribution must be displaced by the concept of "direct ecological salt action." He pointed out that *S. herbacea* has an optimum growth between 1.5 and 3 percent salt. Webb (1966) also pointed out that *Salicornia* plants grown without salt soon die. Waisel (1972) stated that the proportion of chlorides to sulfates and the total salt content were important in determining distribution. For example, *S. herbacea* was more sensitive to a high proportion of sulfates than was *Aster tripolium.*

The fact that Site 1 is an ecotone between *S. pacifica* and *Distichlis stricta* suggests that differences in this site compared with the other two sites would provide information regarding some parameters of *S. pacifica. Distichlis stricta* in this site appears to tolerate a higher pH than *S. pacifica* and may survive in pH values from 8.0 to 9.0. The soil pH apparently affects the availability of nutrients. At pH values over 7 the availability of manganese, iron, copper, molybdenum, and zinc declines (Buckman and Brady, 1969). At high pH values phosphorus forms insoluble complexes of calcium that are unavailable to the plants (Buckman and Brady, 1969). Levitt (1972) also pointed out that *Allenrolfea* *occidentalis* and *S. subterminalis* are highly resistant to salt but sensitive to alkalinity. A change from saline to sodic soils may kill these plants. Site 3, where *S. pacifica* cover and production were the highest, had an average pH of 7.7 and a moisture content of 32 percent. At Site 1 reduction in the soil moisture and the increase in the total concentration of salts of the subsurface soil layers during the season apparently also favored growth of *D. stricta* over *S. pacifica*. *Distichlis stricta* appears to be a better competitor for low soil moisture than *S. pacifica*. It seems probable that during the initial adaptation of *Salicornia* to the saline environment competition played a major role in determining plant distribution. As natural selection of *Salicornia* occurred, adaptations allowing the plant to maintain itself in an optimal salt concentration were reinforced. Plasticity could be reduced and that portion of the gene pool lost that allowed the plant to move back into non-saline areas. As such selective forces would be localized, it would be improper to generalize and say that all species of *Salicornia* have optimum growth at high salt concentration. The variations in salt concentrations that yield optimum growth of *Salicornia* would bear this out (Halket, 1915; Webb, 1966; Levitt, 1972; Waisel, 1972).

The Nature of the Fleshy Stem

Anatomical investigations with light microscopy indicate that as internodes mature or become injured a phellogen that produces fibers and suberized cells is formed in the central stelar region (unpublished results). These cells seal off the conductive tissues from water and nutritive loss as the internodes wither and die. This development would protect the plant when the salt and moisture stresses are the greatest near the surface in July and August.

Osmotic potential measurements of the plants indicated that each internode is probably osmotically independent from other internodes. This would allow the plant to survive in the environment if a few of the internodes were attacked and destroyed by insects or disease. Hill (1908) showed that osmotic adaptation differs not only between species but also between organs and even between cells. In his investigation root hairs varied greatly in this respect, even in the same individual plant. Measurements of freezing-point depression of *S. pacifica* internodes indicated that at least two areas of osmotically different tissues were present within one internode, corresponding to the inner "cortex" and outer chlorenchyma tissues. Osmometer measurements on dissected portions of these tissues indicated that the chlorenchyma tissue had a higher osmotic potential. Scholander *et al.* (1966) suggested that xylem sap of *S. pacifica* may contain very little salt as freezing-point depression of *S. pacifica* sap was found to approach freezing-point depression of pure water. Since chloride ions were equally distributed in these two tissues (unpublished data), the difference was probably due to sodium ions or sugars and other organic molecules that were produced by chloroplasts in the immediate vicinity. Steiner (1935) has shown that chloride ions account for 67 to 88 percent of the increase in osmotic potential of different species of salt marsh plants, whereas other osmotically active substances had only negligible effects. This increase in chloride was shown to account for increases in the osmotic potential of the entire plant. This does not rule out the possibility that differences in osmotic potentials of individual tissues might be due to other osmotically active substances. Increase in the chloride and sodium content of the succulent tissues appears to be the primary means of osmotic adaptation whereby the plant can survive under increased salt and moisture stress. Sodium and chloride ions account for 85 to 95 percent of the osmotic potential of *S. pacifica*. These results agree with the findings of Harward and McNulty (1965) and Scholander *et al.* (1966). Ion analysis of *S. Pacifica* tissues in Site 1 indicated that increases in osmotic potential were due to increases in Na^+ but not Cl^-. Increases in osmotic potential at Site 2 were due to both Na^+ and Cl^-. However, at Site 3 there was a decrease in both Na^+ and Cl^-. As the concentration of the soil salts increased, causing an increase in moisture stress, osmotic potential of the plant also increased. This increase was due chiefly to ions other than Na^+ and Cl^- or sugars and other organic molecules.

Ion analysis of *S. pacifica* tissues showed that the chloride ion was present in higher concentrations than sodium or potassium ions. Azizbekova and Babaeva (1970) found that the amount of absorbed Na$^+$, Cl$^-$, and Mg^{++} in *Salicornia* increased with increasing salt concentrations.

During the period of greatest moisture stress, from July through September, the percentage of crude protein in *S. pacifica* for all three sites remained constant at about 8 percent of the dry weight. The percentage ion content of sodium, potassium, and chloride also remained relatively constant throughout the growing season, even when environmental stresses fluctuated considerably.

The metabolism of *S. pacifica* functioned even with changes in the ionic balance and concentration of ions in the plant. The changes, however, were gradual.

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NEW RECORDS OF STONEFLIES (PLECOPTERA) FROM NEW MEXICO[1]

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Abstract.— Distributional data are presented for 30 species of New Mexico Plecoptera including 8 species new to the state list. Previously, many of the included species were known from a single location in the state. A revised checklist of 46 confirmed species is presented for the state.

Distributional data on the New Mexico stonefly fauna have accumulated slowly because of the isolated nature of much potential stonefly habitat. Records of winter-emerging forms are particularly meager, with three species of Capniidae listed for New Mexico in a review of southwestern stoneflies by Stewart et al. (1974). Two species were recorded from a single location and the other from two locations in the state.

In this paper we report eight additional species, *Malenka flexura* (Claassen), *Podmosta delicatula* (Claassen), *Zapada haysi* (Ricker), *Capnia confusa* Claassen, *Capnia gracilaria* Claassen, *Paraleuctra rickeri* Nebeker and Gaufin, *Diura knowltoni* (Frison), and *Isogenoides zionensis* Hanson; new distributional data for species previously reported are also given. Two of us (Stark and Wolff) collected all material unless otherwise noted.

The authors thank M. R. Cather for providing records from her personal collection, and R. W. Baumann for sending records from the United States National Museum.

Taenionema nigripennis (Banks).—New Records: *Sandoval Co.*, Santa Clara Canyon, Wem Povi Pond, elev. 6,900', 20-III-73, nymphs. *Santa Fe Co.*, Big Tesuque Creek, Big Tesuque Campground, elev. 9,700', 21-IV-73, nymphs; Rio Enmidio, Hyde Park Ski Basin, 10-VI-74, 1 ♂.

Malenka coloradensis (Banks).—New Records: *Catron Co.*, Willow Creek, Willow Creek Campground, 11-VI-74, 2 ♂ 1 ♀. *Sandoval Co.*, Tschicoma Pond, Santa Clara Canyon, 13-VI-74, 3 ♂ 9 ♀.

Malenka flexura (Claassen).—Distribution: *Taos Co.*, West Fork Red River, Wheeler Peak Wilderness Area, 10 miles south of Red River, 9-VI-74, 25 ♂ 14 ♀.

Podmosta delicatula (Claassen).—Distribution: *Rio Arriba Co.*, Rio Chama, Chama, elev. 7,870', 8-VI-74, 9 ♂ 19 ♀. *Taos Co.*, Red River, 2 miles east of Red River, 9-VI-74, 1 ♀.

Prostoia besametsa (Ricker).—New Records: Santa Fe Co., Rio Santa Cruz, near Espanola, elev. 5,600', 17-III-74, 1 ♂; Big Tesuque Creek, Big Tesuque Campground, elev. 9,700', 17-III-74, exuvium.

Zapada cinctipes (Banks).—New Records: *Sandoval Co.*, Santa Clara Canyon, Wem Povi Pond, elev. 6,900', 20-III-73, 1 ♀. Santa Fe Co., Big Tesuque Creek, Big Tesuque Campground, elev. 9,700', 21-IV-73, 5 ♂ 10 ♀.

Zapada frigida (Claassen).—New Records: *Santa Fe Co.*, Big Tesuque Creek, Big Tesuque Campground, elev. 9,700', 10-VI-74, 1 ♂.

Zapada haysi (Ricker).—Distribution: *Lincoln Co.*, North Fork Ruidoso River, 17-V-72, S. M. Fiance, 1 ♀, nymphs. *Santa Fe Co.*, Big Tesuque Creek, Big Tesuque Campground, elev. 9,700', 10-VI-74, 2 ♂ 5 ♀; same location, 21-IV-73, nymphs; Rio Enmidio, Hyde Park Ski Basin, 10-VI-74, elev. 10,560', 2 ♂ 7 ♀. *Taos Co.*, Wheeler Peak, 15 to 25-VI-60, Burks and Kinzer, 1 ♂ 1 ♀; 4 miles north of Arroyo Seco, 22-VI-61, S. G. Jewett, Jr., 2 ♂ 1 ♀; Rio Hondo, Taos Ski Valley, 22-III-67, R. W. Baumann, nymphs; Rio Trampas, above El Valle, 10-VI-74, 2 ♂ 8 ♀; West Fork Red River, Wheeler Peak Wilderness Area, 10 miles south of Red River, 9-VI-74, 3 ♂ 4 ♀.

Capnia confusa Claassen.—Distribution: *Rio Arriba Co.*, Rio Chama, Chama, elev. 7,870', 19-IV-73, 13 ♂ 9 ♀. *Sandoval Co.*, Santa Clara Canyon, Wem Povi Pond, elev. 6,900', 20-III-73, 2 ♂. *San Miguel Co.*, Pecos River, Tererro, elev. 7,600', 21-IV-73, 26 ♂ 10 ♀. *Taos Co.*, Rio Trampas, 1½ miles southeast of El Valle, elev. 7,800', 20-IV-73, 1 ♀.

Capnia gracilaria Claassen.—Distribution: *Santa Fe Co.*, Big Tesuque Creek,

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[1] Study supported by EPA Grant 3053-364 and NSF Grant 6986-609.

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Big Tesuque Campground, elev. 9,700', 21-IV-73, 3 ♂ 13 ♀; same location, 17-III-74, 2 ♂; Rio Enmidio, Hyde Park Ski Basin, elev. 10,560', 10-VI-74, 2 ♀. *Taos Co.*, West Fork Red River, Wheeler Peak Wilderness Area, 9-VI-74, 1 ♂ 1 ♀.

Eucapnopsis brevicauda Claassen.—New Records: *Santa Fe Co.*, Big Tesuque Creek, Big Tesuque Campground, elev. 9,700', 21-IV-73, 1 ♂.

Paraleuctra rickeri Nebeker & Gaufin.—Distribution: *Taos Co.*, West Fork Red River, Wheeler Peak Wilderness Area, 10 miles south of Red River, 9-VI-74, 12 ♂ 26 ♀.

Paraleuctra vershina Gaufin and Ricker.—This species has been previously reported from the state as *P. sara* (Claassen). New records: *Rio Arriba Co.*, Rio Chama, Chama, elev. 7,870' 8-VI-74, 2 ♂ 2 ♀. *Taos Co.*, Rio Trampas, above El Valle, 9-VI-74, 6 ♂ 11 ♀.

Pteronarcella badia (Hagen).—New Records: *Sandoval Co.*, Santa Clara Canyon, Wem Povi Pond, elev. 6,900', 20-III-73, nymphs.

Diura knowltoni (Frison).—Distribution: *Rio Arriba Co.*, Rio Chama, Chama, elev. 7,870', 8-VI-74, 2 ♂ 6 ♀; same location, 25-V-74, M. and E. Cather, nymphs. *Taos Co.*, Rio Trampas, 1½ miles southeast of El Valle, elev. 7,800', 20-IV-73, nymphs.

Isogenoides elongatus (Hagen).—New Records: *San Miguel Co.*, Pecos River, Pecos, 24-V-74, M. and E. Cather, 5♂ 5 ♀.

Isogenoides zionensis Hanson.—Distribution: *Catron Co.*, San Francisco River, Glenwood, 19-II-70, M. Snavely, nymph. *McKinley Co.*, McGaffey Lake, 10-IV-70, nymph. *Rio Arriba Co.*, Rio Chama, Chama, elev. 7,870', 19-IV-73, 1 ♂ (reared); same location, 8-VI-74, 6 ♂ 2 ♀. *Taos Co.*, Red River, Red River, 5-III-61, A. R. Gaufin, nymph; Red River, 3 miles east of Cuesta, 9-VI-74, nymphs.

Kogotus modestus (Banks).—New Records: *Taos Co.*, Red River, 2 miles east of Red River, 9-VI-74, nymphs.

Megarcys signata (Hagen).—New Records: *Santa Fe Co.*, Big Tesuque Creek, Big Tesuque Campground, elev. 9,700', 21-IV-73, nymphs; same location, 10-VI-74, 46 ♂ 1 ♀; Rio Enmidio, Hyde Park Ski Basin, elev. 10,560', 17-III-74, nymphs. *Taos Co.*, Rio Trampas, 1½ miles southeast of El Valle, elev. 7,800', 20-IV-73, nymphs; West Fork Red River, Wheeler Peak Wilderness Area, 9-VI-74, nymphs.

Skwala parallela (Frison).—New Records: *Taos Co.*, Rio Hondo, Hwy. 3, 5-III-61, A. R. Gaufin, nymphs.

Isoperla ebria (Hagen).—New Records: *Santa Fe Co.*, Big Tesuque Creek, Big Tesuque Campground, elev. 9,700', 10-VI-74, 1 ♂; same location, 21-IV-73, nymphs; Rio Enmidio, Hyde Park Ski Basin, elev. 10,560', 17-III-74, nymphs.

Isoperla fulva Claassen.—New Records: *Santa Fe Co.*, Big Tesuque Creek, Big Tesuque Campground, elev. 9,700', 21-IV-73, nymphs.

Isoperla mormona Banks.—New Records: *Catron Co.*, Whitewater Creek, Catwalk Picnic Area, 11-VI-74, 1 ♂; West Fork Gila River, 17-V-74, M. and E. Cather, 15 ♂ 6 ♀. Grant Co., Gila River, 31 miles north of Pinos Altos, Hwy 15, 11-VII-73, 1 ♂ (reared); same location, 17-V-74, M. and E. Cather, 26 ♂ 17 ♀.

Claassenia sabulosa (Banks).—New Records: *San Miguel Co.*, Pecos River, Tererro, elev. 7,600', 21-IV-73, nymphs.

Hesperoperla pacifica (Banks).—New Records: *Catron Co.*, Whitewater Creek, 16-V-74, M. and E. Cather, exuvium.

Sweltsa coloradensis (Banks).—New Records: *Catron Co.*, Willow Creek, Willow Creek Campground, 11-VI-74, 8 ♂ 7 ♀. *Rio Arriba Co.*, Rio Chama, Chama, elev. 7,870', 8-VI-74, 1 ♂ 3 ♀. *Sandoval Co.*, Tschicoma Pond, Santa Clara Canyon, 13-VI-74, 2 ♀.

Sweltsa lamba (Needham & Claassen).—New Records: *Taos Co.*, West Fork Red River, Wheeler Peak Wilderness Area, 10 miles south of Red River, 9-VI-74, 1 ♂.

Triznaka diversa (Frison).—New Records: *Santa Fe Co.*, Big Tesuque Creek, Big Tesuque Campground, elev. 9,700', 10-VI-74, 31 ♂ 24 ♀.

Triznaka pintada (Ricker).—New Records: *Taos Co.*, Rio Pueblo, Penasco, 9-VI-74, 2 ♂ 13 ♀.

Triznaka signata (Banks).—New Records: *Rio Arriba Co.*, Rio Chama, Chama, elev. 7,870', 8-VI-74, 17 ♂ 10 ♀.

New Mexico List

Below is a checklist of 46 stonefly species that have been confirmed for New Mexico. Species regarded as questionable or unconfirmed by actual specimens and distributional data have been omitted.

Taeniopterygidae
Taenionema nigripennis (Banks)
T. pallida (Banks)
Taeniopteryx sp.
Nemouridae
Amphinemura mogollonica Baumann and Gaufin
Malenka coloradensis (Banks)
M. flexura (Claassen)
Podmosta delicatula (Claassen)
Prostoia besametsa (Ricker)
Zapada cinctipes (Banks)
Z. frigida (Claassen)
Z. haysi (Ricker)
Capniidae
Capnia confusa Claassen
C. fibula Claassen
C. gracilaria Claassen
Eucapnopsis brevicauda Claassen
Mesocapnia frisoni (Baumann and Gaufin)
Leuctridae
Paraleuctra rickeri Nebeker and Gaufin
P. vershina Gaufin and Ricker
Perlomyia utahensis Needham and Claassen
Pteronarcidae
Pteronarcella badia (Hagen)
Pteronarcys californica Newport
Perlodidae
Cultus aestivalis (Needham and Claassen)
Diura knowtoni (Frison)
Isogenoides elongatus (Hagen)
I. zionensis Hanson
Kogotus modestus (Banks)
Megarcys signata (Hagen)
Skwala parallela (Frison)
Isoperla ebria (Hagen)
I. fulva Claassen
I. longiseta Banks
I. mormona Banks
I. patricia Frison
I. phalerata (Smith)
I. quinquepunctata (Banks)
Perlidae
Claassenia sabulosa (Banks)
Hesperoperla pacifica (Banks)
Neoperla clymene (Newman)
Chloroperlidae
Paraperla frontalis Banks
Suwallia pallidula (Banks)
Sweltsa borealis (Banks)
S. coloradensis (Banks)
S. lamba (Needham and Claassen)
Triznaka diversa (Frison)
T. pintada (Ricker)
T. signata (Banks)

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STEWART, K. W., R. W. BAUMANN, AND B. P. STARK. 1974. The distribution and past dispersal of southwestern United States Plecoptera. Trans. Amer. Entomol. Soc. 99:507-546.

THE AUTHORSHIP AND DATE OF PUBLICATION OF *SIREN INTERMEDIA* (AMPHIBIA: CAUDATA)

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ABSTRACT.— However "just" it might be to credit LeConte, 1828, with *Siren intermedia*, both Harlan, 1826 (not 1827 as often cited), and Barnes, 1826, antedate LeConte's proposal of the name. As the earliest, Barnes, 1826, stands credited with it. In analysis of precedent for these conclusions, types of taxonomic plagiarism (calculated vs. innocent, homoplagiarism vs. heteroplagiarism) and the distinctions between *nomina nuda* and *nomina dubia* are reviewed, giving examples of each category.

Martof (1973: 1-3), in the most recent review of *Siren intermedia*, notes that the earliest full description of the species in LeConte (1828: 133-134, pl. 1) actually was antedated by a brief but nominally occupying characterization, credited to LeConte, that appeared in a work by Harlan (1826: 322), dated 1827 by Schmidt (1953: 14) and others.

Two points merit observation in this context: (1) the particular page on which the "description" of *Siren intermedia* appeared in Harlan's work was actually published in 1826, *fide* the 1913 Index to the Scientific Contents of the Journal and Proceedings of the Academy of Natural Sciences of Philadelphia, p. viii; and (2) there is reason to accept the author of this "description" as Harlan, not LeConte. Harlan "read" his paper at the 12 Dec. 1826 meeting of the Academy, and accordingly the pages published in 1826 (pp. 317-324) must have appeared sometime after 12 Dec., the remainder (pp. 325-372) in February 1827, according to the Index. The article was completed in no. 1 of vol. 6 of the Journal (pp. 7-38) appearing in March 1827 *fide* the same source.

The author of the description appearing in Harlan (1826: 322) is clearly Harlan, not LeConte, despite the fact that Harlan attributed the name to LeConte and stated (in a footnote) that the material on this species was sourced from "manuscript notes." The characterization obviously was written by Harlan, not LeConte, as becomes evident when one consults LeConte's formal description that appeared in 1828. Harlan seemingly saw the LeConte ms. and published in his own words the name and certain characters cited in the ms. The acknowledgment of source does not nullify applicability of Art. 50 of the International Code of Zoological Nomenclature (ICZN, 1964: 49), which states, "The author . . . of a scientific name is . . . the person . . . who first publishes it in a way that satisfies the criteria of availability, unless it is clear from the contents of the publication that . . . some other person is *alone* responsible for both the name and the conditions that make it available" (italics ours).

LeConte obviously was responsible for the name but equally clearly was not responsible for the "description" that "satisfies the criteria of availability." Harlan obviously wrote the description; and despite his apparent wish to the contrary, the present rules would require that he be regarded as author of the name in zoological nomenclature if indeed his account were the earliest to have appeared.

There is ample precedent for crediting the immediate source of any given name and its characterization, however questionable may be the derivation of either, for that name. This policy unfortunately rewards plagiarism with permanence unless the International Commission on Zoological Nomenclature intercedes. On the other hand, plagiarism seldom occurs, either inadvertently or deliberately. Nevertheless, it does occur on occasion, and the Code requires that the perpetrator bear responsibility for his act, whether it be innocent or calculated. Examples of calculated plagiarism are provided by Thompson's three privately printed notices of 1912; the first two antedated Van Denburgh's competitive advance diagnosis of 1912, and although Thompson's descriptions are sourced directly from Van Denburgh's manuscript, insofar as they antedate Van Denburgh's descriptions they are accepted under the Code as valid (see Barbour, 1917, for details).

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Examples of innocent taxonomic plagiarism fall into two categories: self-plagiarism (or homoplagiarism) and heteroplagiarism. A medium for frequent homoplagiarism is Dissertation Abstracts, wherein summaries of doctoral dissertations occasionally include sufficient information with a new name or a new combination to occupy them; for example Walker's abstract (1967) includes sufficient information on two new names (*Cnemidophorus gularis rauni*, *C. g. semiannulatus*) to occupy both, whereas it was intended that these names not be entered into nomenclature before full documentation could be provided (full descriptions have not even yet appeared). A similar case occurred in another journal (Harris, 1974), wherein a photograph and brief notice of some characteristics of a new subspecies of rattlesnakes was accompanied by a name (*Crotalus willardi obscurus*), thus occupying the name in advance of the intended date and work which was then in press.

An example of heteroplagiarism occurred with inadvertent mention of *Palmatotriton* by Smith (1945), who used the name under the impression that his former professor, E. H. Taylor, had a ms. in press establishing the genus, and that the casual mention in the popular journal would be meaningless. Unfortunately Taylor had decided against erection of the genus, and, more regrettably, Smith's use of the name was accompanied by a few incidental comments inadvertently serving to occupy the name nomenclaturally. It was necessary to appeal to the International Commission on Zoological Nomenclature to "deoccupy" *Palmatotriton* as of Smith, 1945, making the name available for use by anyone else, in any desired sense (ICZN, 1956).

In all these examples, including that of Harlan, it is clear that intent has nothing to do with result; only the briefest characterization, in but a few words, may serve to occupy a name even when not so intended, and the person responsible is the one presenting those words, even though he may not have intended to receive that responsibility.

In this context it is important to recognize that a name may be occupied even though its characterization may be inadequate for definitive allocation to its proper taxon in nature; such names are *nomina dubia* despite the fact that they are occupied names. There is a rather wide misapprehension that a full characterization is required in order to occupy a new name, but this is not so. *Nomina dubia* are often rendered identifiable (i.e., *nomina clara*) by subsequent provision of further details, as is true in the case of *Siren intermedia.* Harlan's description, although adequate to occupy the name were it the original usage, would not alone have sufficed for allocation; but with LeConte's full account, no doubt remains. As of Harlan, *Siren intermedia* is a *nomen dubium*; as of LeConte, it became a *nomen clarum* although occupied at an earlier date by another author. Harlan's usage was not of a *nomen nudum*, which is nonexistent nomenclaturally, because it *did* provide some distinguishing information. The Code makes clear (Art. 13) that *any* "statement that purports to give characters differentiating the taxon" (italics ours) suffices to occupy an accompanying name, and practice has conformed with this liberal rule.

In the case of *Siren intermedia*, however, the comedy of errors did not really begin with Harlan, even of 1826. There is a still earlier usage that occupied the name. Barnes (1826: 269, footnote) saw or otherwise knew of LeConte's ms and rendered the name *Siren intermedia* available in almost precisely the same way that Harlan's work would have done had it been the earliest usage. The Barnes footnote follows: "*Additional note communicated by the author, Aug. 15, 1826.* The delay in the printing of this paper has given the author an opportunity of announcing, in this place, the discovery of ANOTHER NEW SPECIES OF SIREN, by Capt. LECONTE. It belongs to this section, and is called by its discoverer *Siren intermedia.* In its color it resembles the *Lacertina*, and in its gills, the *Striata;* but it has peculiar characters of its own, which will be explained at length in a paper soon to be published in the Annals of the Lyceum. Length about one foot, inhabits the Southern states in large numbers. Specimens are preserved in the Cabinet of the Lyceum. Fig. Annals of the Lyceum, Vol. 2, fig. 1." That Barnes knew of LeConte's description long before its publication is not surprising, inasmuch as he was the "Recording Secretary of the New York Lyceum," as indicated (p. 268) in his 1826 paper. Only by the close familiarity permitted by such an association could he have known some two years in advance of publication that LeConte's account would appear in Volume 2 and incorporate Figure 1 of the Annals of the Lyceum!

The Harlan and Barnes works were both dated 1826, but the Harlan paper appeared very late in the year—certainly after December 12—whereas the Barnes paper, read before the Lyceum in July 1825, was surely published shortly after 15 August 1826, when Barnes inserted his footnote on *S. intermedia*. We have not been able to pinpoint the exact date of publication of either work, but the evidence that Barnes' work preceded that of Harlan is overwhelming.

The same generalities pertinent to Harlan's use of the name *Siren intermedia* are equally pertinent to the earlier Barnes usage. Barnes actually must be regarded as the author of *Siren intermedia* (which accordingly dates from 1826), unless the case is appealed to the ICZN, asking for rejection of the contributions of both Barnes and Harlan on that species, giving LeConte (1828) priority. The effort is not warranted, however, since the significance of the case is grossly inadequate to justify the protracted, laborious protocol involved in ICZN action. Custom dictates that suspension of the rules be requested only for names of relatively broad familiarity among zoologists; the present certainly does not fall into that category.

We are accordingly left with the conclusion that the proper citation for the species under consideration is *Siren intermedia* Barnes, 1826.

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NEW MITES FROM THE YAMPA VALLEY[1]
(ACARINA: CRYPTOSTIGMATA: ORIBATULIDAE, PASSALOZETIDAE)

Harold G. Higgins[2] and Tyler A. Woolley[3]

ABSTRACT.— A study was made of the soil mites from under different vegetative types near a coal-burning power plant in the Yampa Valley near Hayden, Colorado. The following new species of oribatids were found: *Zygoribatula apletosa* n.sp., *Multoribates haydeni* n.sp., *Paraphauloppia cordylinosa* n.sp., *Passalozetes moniles* n.sp.

Concentrated collections have been made near a coal-burning power plant in the Yampa Valley near Hayden, Colorado. A number of new and unrecorded species of soil mites for Colorado have been found in the project area. The collections were made with reference to the soil forms and to vegetative types with which they were found. As might be expected, many species appear to be more abundant at one season of the year than at another or may be more closely associated with certain vegetative types than with others.

This concentrated collecting over a two-year period has given new insight as to the importance of the microclimate in the biology of oribatids. For example, depending on the amount of moisture, sunlight or shade, and slope, many species may be more abundant under one side of a bush than under the other. Preliminary studies also indicate that destruction of vegetation and disturbances of the soil in such changes as the formation of spoil banks or strip-mining and pollution from coal-burning power plants seriously depletes the numbers and kinds of soil arthropods.

Following are descriptions of four new species representing two families of oribatids found in the Hayden area.

FAMILY ORIBATULIDAE

Zygoribatula apletosa, n.sp.

Figs. 1 and 2

DIAGNOSIS.— Large size, larger than any known *Zygoribatula*; with 14 pairs of large, setose notogastral setae; rostral hairs further apart than lamellar hairs; lamellae curved inward with distinct translamella; areae porosae *Aa* located near the small shoulder projections. The trivial name *apletosa* is modified from the Greek, and implies "immense," referring to the size of these oribatids.

DESCRIPTION.— Color reddish-brown; rostrum rounded; rostral hairs heavy, reaching beyond tip of rostrum by about half their lengths, hairs farther apart than lamellar setae; lamellae of almost uniform width throughout, length curved inward toward anterior tip, slightly less than one-half as far apart at tip as at base; translamella narrower than lamellae; lamellar hairs similar to rostral hairs but about one-third longer inserted in anterolateral ends of lamellae; interlamellar hairs situated midway between insertions of lamellar hairs and pseudostigmata, closer to inner margin of lamellae; pseudostigmata cuplike with edge erected above surface of prodorsum; sensillum with broad, rounded setose head and short pedicel, about half as long as interlamellar hair; exobothridial hair rather heavy and stiff.

Hysterosoma longer than broad, widest near middle, with tapering posterior end; dorsal surface with 14 pairs of heavy, long, spined setae, many extending beyond body outline as shown in Figure 1; areae porosae all large, *Aa* much longer than broad and located near small humeral process.

Camerostome oval in outline; ventral surface with apodemata and setae as shown in Figure 2; genital and anal apertures far apart, smaller genital opening more than twice its length anterior to larger anal aperture; each genital cover with four setae; aggenital setae as shown in Figure 2; each anal cover with two setae (2 of 12 specimens with 3 anal setae); two adanal setae present.

Legs all about equal in size; heterotridactylous, median claw larger than laterals.

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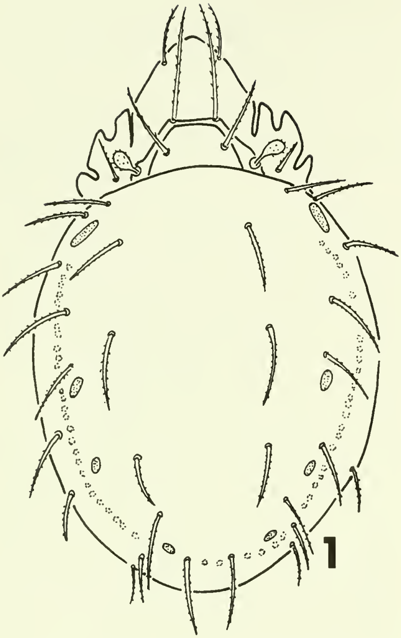

Fig. 1. *Zygoribatula apletosa*, dorsal aspect, legs omitted.

Measurements.— length .705 mm; width, .495 mm. (Range .853-.705 mm X .600-.495 mm). The type (a male) and 6 paratypes (6 females) were taken under serviceberry about ¼ mile NE power plant, Hayden, Colorado, 7 Oct. 1971, by H. G. Higgins; 2 specimens, females, were taken under rosebush, ½ mile N power plant, Hayden, Colorado, 21 June 1972; 2 specimens (males) were taken ½ mile N power plant, Hayden, Colorado, 1 Aug. 1971; 1 specimen (male) was taken under aspens, 4 miles S Seneca Road, Hayden, Colorado, 1 Aug. 1971; all by H. G. Higgins.

Discussion.— This species stands apart from other known North American *Zygoribatula* by its large size, its long, heavy, setose body setae, and by its big, long, areae porosae *Aa* located near the shoulder. In general appearance *Z. apletosa* n.sp. resembles *Z. lata* Hammer but differs in the much larger size as well as in the size and locations of areae porosae.

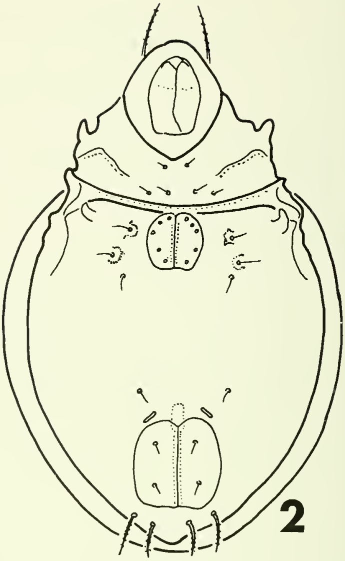

Fig. 2. *Z. apletosa*, ventral aspect.

To date, this species has always been found associated with rather heavy, moist litter under dense vegetation.

This species shows interesting variation in the width of the translamellae and location of body setae. Also, as pointed out earlier, 2 of 12 specimens have 3 pairs, rather than 2 pairs, of anal setae.

Multoribates haydeni, n.sp.

Fig. 3

Diagnosis.— Similar to *Multoribates chavinensis* Hammer, 1961, but larger, and with only 11 pairs of dorsal setae; lacks the ventral keel on femur II. The trivial name is indicative of location.

Description.— Large size; color yellowish to light brown; body egg-shaped with the pteromorphs hardly projecting beyond lateral outline of body; prodorsum triangular in outline with rostrum fairly pointed, often hyaline; rostral setae inserted posteriorly on lateral margins of propodosoma, much wider apart than lamellar hairs; lamellae narrow, tapering slightly anteriorly; translamellae absent; lamellar hairs stiff, setose about same length as lamellae; interlamellar hairs

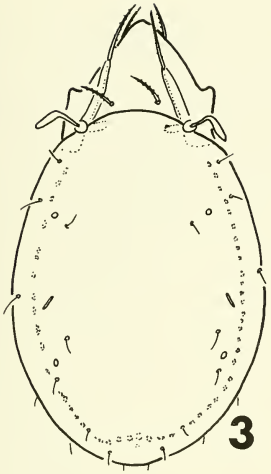

Fig. 3. *Multoribates haydeni,* dorsal aspect, legs omitted.

heavy, nearly equal in length to lamellar hairs; pseudostigmata cuplike, rim projecting beyond the body level; sensillum with narrow stalk and broad, setose head that is bent backwards; dorsosejugal suture curved anteriorly.

Hysterosoma longer than broad with small pteromorphs that project only slightly beyond the outline of body; 11 pairs of fine, simple dorsal hairs visible as shown in Figure 3; areae porosae absent, but replaced with chitinous pores; muscle scars and markings visible round edge of hysterosoma as indicated in Figure 3. Variations occur in the locations of body setae.

Ventral surface similar to *M. chavinensis* with only a few minor exceptions; genital plates separated from larger anal plates by approximately twice their length, each plate with four setae; anal plates much larger than genital plates, situated near posterior end of body, each anal plate with two hairs; adanal and aggenital setae place similarly to *M. chavinensis;* fissure *iad* located near anteromediad margin of anal plates.

Legs about equal in size; all legs heterotridactylous, median claw larger than laterals; femur II without visible keel.

Measurements.— Length, .45 mm; width, .26 mm. The type, a gravid female was collected at Seneca #2, Hayden, Colorado, under serviceberry, 10 April 1971, by H. G. Higgins and T. A. Woolley. Additional specimens are as follows: 1 specimen at Seneca #2, Hayden, Colorado, 9 June 1971, in sagebrush, by T. A. Woolley and H. G. Higgins; 3 specimens from under aspens associated with bitterbrush (*Purshia*), 8 June 1971, 4 miles S Seneca Road, Hayden, Colorado, by H. G. Higgins and T. A. Woolley; 6 specimens from under bitterbrush, 5 miles S Seneca Road, Hayden, Colorado, 1 Aug. 1971, by H. G. Higgins; 8 specimens from under bitterbrush, 5 miles S Seneca Road, Hayden, Colorado, 8 Oct. 1971, by H. G. Higgins; 1 specimen from under bitterbrush, 4 miles S Seneca Road, Hayden, Colorado, 21 June 1972, by H. G. Higgins.

Discussion.— In general appearance *M. haydeni*, n.sp. resembles *M. chavinensis* Hammer but is larger, lacks the ventral keel on femur II, and has 11 rather than 14 pairs of dorsal setae. Preliminary study seems to indicate that although this new species is found in several habitats, it prefers the microhabitat under bitterbrush in rather arid conditions.

Paraphauloppia cordylinosa, n.sp.

Fig. 4

Diagnosis.—Similar in outline to *Paraphauloppia novazealandica* Hammer, 1967, but with much larger lamellae and 11 pairs of notogastral hairs. The name *cordylinosa* refers to the clublike sensillum of the new species.

Description.— Color yellowish; rostral setae large, rough, situated on the anterolateral margins of the propodosoma; lamellae quite large, extended more than half the length of propodosoma, about equal in width throughout theirs lengths, with a small spur (prolamella) located anteromediad; lamellar hairs inserted in anterior tip of lamellae, extending to tip of rostrum, heavy, barbed, and about equal in length to rostral hairs; interlamellar hairs three-fourths as long as lamellar hairs, inserted mediad, closer to pseudostigmata than to tip of lamellae extending to the sides of prodorsum; pseudostigmata cuplike with a short stalk and expanded, rounded, setose head.

Hysterosoma oval, tapering anteriorly; dorsosejugal suture greatly arched; ptero-

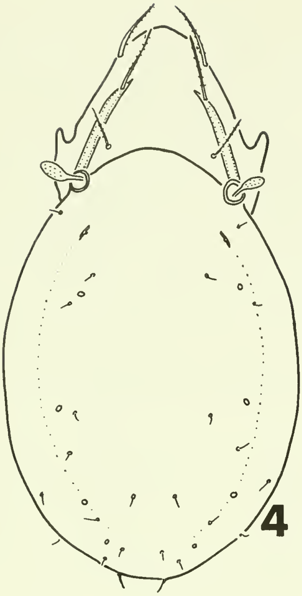

Fig. 4. *Paraphauloppia cordylinosa*, dorsal aspect, legs omitted.

morphs absent; 11 pairs of simple smooth, dorsal hairs as shown in Figure 4. Areae porosae visible but not noticeably enlarged as in *P. novazealandica;* a line of light marking, probably muscle scars, visible mediad of lateral margins.

Anal opening much larger than genital opening and situated near posterior end of body, each cover with two setae; genital opening smaller, situated about twice its length in front of anal opening, three pairs of visible hairs on each plate; aggenital setae posterior to genital plate; aggenital and adanalsetae located similarly to *P. novazealandica*, ad_1 posterior to anal plate, ad_2 situated near the middle of plate along lateral side, and ad_3 situated anterior to anal plate.

All legs about equal in size, heterotridactylous, with median claw larger than laterals.

Measurements.— Length, 282μ; width, 132μ. The type (a female) and a paratype from sagebrush, Yampa Airport, Hayden, Colorado, 9 June 1971; 6 specimens from sagebrush, 2 miles S Yampa Airport, Hayden, Colorado, 9 June 1971; all by H. G. Higgins and T. A. Woolley.

Discussion.— In general appearance this species resembles *P. novazealandica* Hammer but differs in having much larger, heavier lamellae and 11 rather than 10 pairs of dorsal setae. Although this taxon differs somewhat from *Paraphauloppia* in the number of dorsal setae, it appears to be nearer this genus than to *Phauloppia.* We hesitate, at this time, to describe a new genus based on these minor differences and because in the small sample of mites collected there is great variation in the exact location of the dorsal setae, and the lengths of the lamellar hair. It is interesting that although collections were made at the same general site several times a year, and over a two-year span, specimens of this species were found only once, in June 1971, and those in rather dry sagebrush habitat. Preliminary postulations attribute this to the possible influence of pollutants in the area.

Family Passalozetidae

Passalozetes moniles, n.sp.

Figs. 5-6

Diagnosis.— This species is readily separated from *P. linearis*, the only other known North American species, by the banded, beadlike pattern of dorsal and ventral integuminal and by the smooth sensillum with a pointed tapered head. The trivial name *moniles* is modified from the Latin meaning "necklace" and refers to the beaded appearance of the integument.

Description.—Yellowish in color; prodorsum slightly wider than long; rostrum blunt, rounded; rostral hairs simple, inserted near tip of rostrum, curved medially toward tip of rostrum; lamellae absent; lamellar hairs small, simple, slightly longer than rostral hairs, curved down toward tip of rostrum; interlamellar hairs threadlike, simple, inserted anteromediad of pseudostigmata, adjacent to coalesced median section of dorsosejugal suture; pseudostigmata cuplike, separated from each other by a little more than length of sensillum; sensillum with a narrow curved base and tapering into a narrow pointed head.

Hysterosoma oval, anterior margin extended forward, coalesced medially with

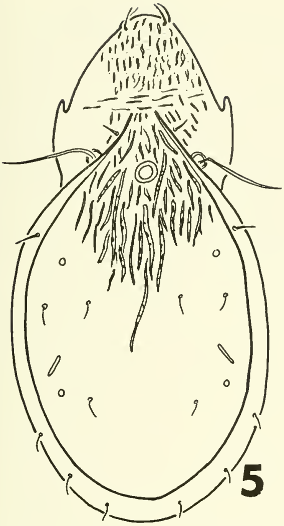

Fig. 5. *Passalozetes moniles*, dorsal aspect, legs omitted.

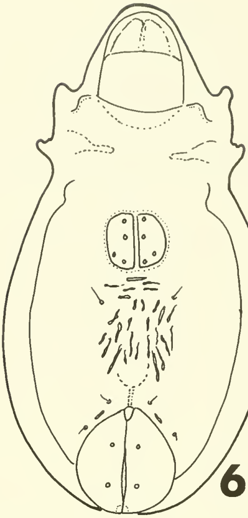

Fig. 6. *P. moniles*, ventral aspect, legs omitted.

dorsum of propodosoma beyond level of interlamellar hairs; dorsosejugal suture interrupted by this middle projection; lenticulus clear, round, surrounded by lines; dorsum with simple hairs as shown in Figure 5. Integument of fine lines with darker pigmented areas resembling strings of beads (the beadlike cerotegument may be removed by soaking in lactophenol); two pairs of area porosae and a glandular fissure as seen in Figure 5.

Camerostome with rather parallel sides, longer than wide; ventral plate as seen in Figure 6; genital covers each with four pairs of genital setae; aggenital setae inserted about twice their lengths posterolaterad of genital aperture; anal aperture nearly one-third larger than anal opening; anal aperture in the posterior end of ventral plate, each cover with two setae; adanal setae difficult to find in the cerotegument, visible setae and glands as shown in Figure 6.

All tarsi heterobidactylous, heavier of the two claws toothed (median or lateral).

Measurements.— Length, .36 mm; width, .15 mm.

The type (a male) and 3 paratypes were taken from under bitterbrush and squawbrush, 6 miles E Craig, Colorado, 14 June 1972; 4 specimens from burned-over area at Seneca #3, Hayden, Colorado, 21 June 1972; all by H. G. Higgins.

Discussion.— As is to be expected, there is considerable variation in the arrangement of setae and pigmentation in specimens examined. Those examples from the burned-over area were more heavily pigmented and have a wider hysterosoma than those taken near Craig. The only previously described *Passalozetes* from this western area was taken from a dry woodrat nest in Tooele Co., Utah, several hundred miles to the west of the location of this new species. Both North American species of Passalozetes have been taken from dry desert sands, which implies that they are found in xeric habitats.

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Higgins, H. G., and T. A. Woolley

THE IDENTITY OF BOCOURT'S LIZARD *EUMECES CAPITO* 1879

Hobart M. Smith[1], Rozella B. Smith[1], and Jean Guibé[2]

Abstract.— *Eumeces capito* Boucourt, 1879, is a senior synonym of *Eumeces xanthi* Günther, 1889. No exception to application of the Law of Priority is recommended in this case. The type locality of *E. capito* as originally published ("La côte oriental des Etats-Unis") is erroneous. Undoubtedly the correct locality is China, but it is not restricted at present.

In preparation of "Synopsis of the Herpetology of Mexico," a problem has arisen: whether or not to apply the name *Eumeces capito* Bocourt (1879:429-431, pl. 22D, Figs. 8, 8a-8c) to some Mexican species. The origin of the only specimen (holotype, no. 5531 of the Muséum National d'Histoire Naturelle, Paris) is in doubt, for although the published locality is "la côte oriental des Etats-Unis," the several registers in the Muséum in Paris give still other indications: "Mexique" and "Amérique septentrionale." The collector is also unknown, for M. S. Braconnier, by whom Bocourt (*loc. cit.*) indicated the specimen was "donné," was merely an assistant in the Muséum, never participating in any expedition; he simply made this and other specimens available for study by Bocourt and other scientific personnel.

Taylor's exhaustive monograph (1936: 28, 231-2, 506) of *Eumeces* sheds no light upon the problem of the identity of *E. capito*, as the type was not examined, and by description alone the name could not be allocated. Taylor did note the possibility that the name applies to his *Eumeces inexpectatus*, 1932, although he thought it "probable that it is based upon an aberrant specimen of *fasciatus*" (p. 232).

We have thus been motivated to reexamine the only specimen constituting the hypodigm for *Eumeces capito*, being made available by the junior author for study by all of us. It proves to be a typical, mature example of *Eumeces xanthi* Günther (1889:218). The specimen is in excellent condition, slightly softened, but not notably damaged, discolored, or faded. Salient data are: snout-vent 72 mm, hind leg 28 mm, foreleg 19 mm, axilla-groin 40 mm, tail 69 mm (30 mm regenerated); 24 scale rows around midbody; 54 scales from parietals to above anus; 16-16 lamellae under 4th toe; a conspicuous patch of enlarged postfemoral scales; one postnasal; two postmentals; parietals narrowly separated posteriorly by tip of interparietal; frontonasal broadly contacting frontal; upper secondary temporal quadrangular, dorsal and lateral edges nearly parallel, separated from 7th (posterior) supralabial by contact of primary temporal and lower, subtriangular secondary temporal; two pairs of nuchals; median preanals overlapped by lateral scales; a somewhat modified, slightly keeled lateral postanal; median subcaudals twice as wide as adjacent scales; a distinct, brown lateral stripe on 4th scale row and edges of adjacent 3rd and 5th rows; a dorsolateral light stripe occupying most of the 3rd scale row; and a lateral light stripe occupying the lower half of the 5th scale row; no evidence of a median light stripe on head, and its only evidence on trunk the absence of dark pigment on the adjacent halves of the 2 median scale rows; other dorsal scale rows with some dark flecking on the base of each scale. Other features as indicated in the accompanying figures.

Most of the characters of this specimen conform with those detailed by Taylor (1936:239-243, Fig. 33, Pl. 15) for *Eumeces xanthi*, and indeed the holotype of *E. capito* closely resembles one of the syntypes figured on his Plate 15 (Fig. 3), although the pigment loss has not attained the level there depicted for a 76 mm specimen. Critical are the modified lateral postanals, the enlarged postfemorals, the low number (24) of scale rows, and the position of the dorsolateral light stripe on the 3rd scale row, in addition to the single postnasal and paired postmentals. No American species of *Eumeces* have enlarged postfemorals; only a few Asiatic species possess them, and all except *E.*

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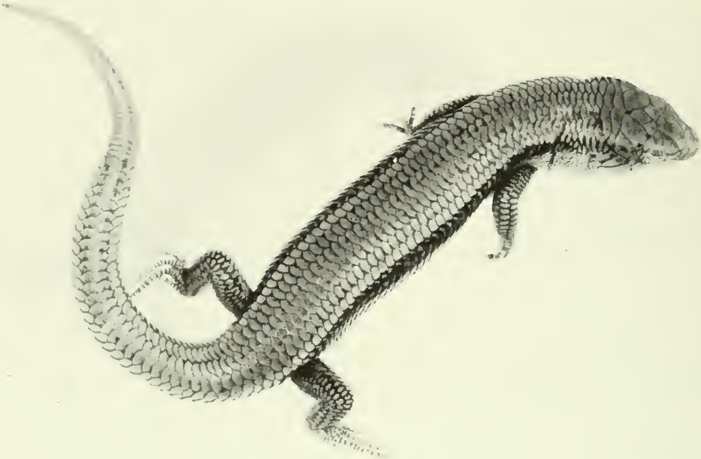

Fig. 1. Holotype of *Eumeces capito* Bocourt, dorsal view.

xanthi are eliminated from consideration by number of scale rows or by the postnasal-postmental characters.

The only notable discrepancy between the holotype of *E. capito* and Taylor's account of *E. xanthi* is the low number of dorsals (54) in the former, as compared with the range (56 to 60) for the latter. However, northern examples of *E. xanthi* tend to have fewer dorsals (56-59, compared with 59-60 for southern examples); nevertheless, northern examples tend to have 22 scale rows, whereas southern ones usually have 24. We suspect that the type of *E. capito* was taken in more northern parts of the species' range, conforming more closely with the geographic variant that bears the name *Eumeces pekinensis* Stejneger (1924:120), type locality Hsin-Lung-Shan district, imperial hunting grounds, Chihli Province, 665 mi N Peking, China, than with the geographic group represented by *Eumeces xanthi* (type locality Ichang, Hupeh, China). The contact of frontonasal with frontal that occurs in the type of *E. capito* conforms with Stejneger's description and figures (1925:49-51, fig. 2) for the three types of *E. pekinensis* and with Taylor's figure (1936:242, fig. 33), in which the two prefrontals are in contact and therefore separate frontal and frontonasal. However, the figured specimen is from the same district as the types of *E. pekinensis;* presumably the character is not taxonomically significant. On the contrary, the number of dorsals and number of scale rows may indeed be significant,

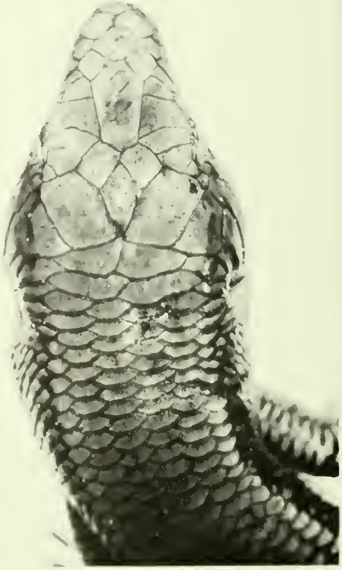

Fig. 2. Dorsal view of head of the holotype of *Eumeces capito* Bocourt.

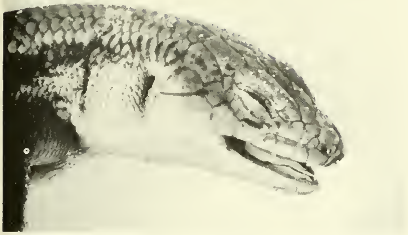

Fig. 3. Lateral view of the head of the holotype of *Eumeces capito* Bocourt. The minute spheres abundantly evident in this figure, and less abundant in Figs. 2 and 4, are air bubbles. All photos were taken of the specimen under water.

at least subspecifically; more material will be required to establish the nature of the variation that occurs in the species. Certainly the low number of dorsals in the type of *E. capito* casts no doubt upon proper allocation with *E. xanthi*, although it may be important in naming the geographic races of that species at some time in the future.

We are not aware of more recent studies of *E. xanthi* that would shed any light upon the geographic variation of that species. The related species *E. tamdaoensis* Bourret (1937:19-21, fig. 5) is very similar and may well be referable to *E. xanthi* as a geographic race, but the original description does not note presence or absence of enlarged postfemorals; a peculiar head pattern of juveniles may be distinctive, as well as the greenish color above and below in life. *Eumeces coreensis* Doi and Kamita (1937:211-215, figs.) is not closely similar, being related more closely to *E. chinensis* (no postnasal, no enlarged postfemorals). However, the wide range of *E. xanthi* (and its close relatives *E. tamdaoensis*, *E. elegans* and *E. tunganus*) suggests that a polytypic species or a species complex may be involved, the nomenclature of which is far from stable.

Because of this primitive state of knowledge of variation in the *xanthi* subgroup (unique in having enlarged postfemorals) of the Asiatic members of Taylor's *fasciatus* group, we regard it unwise to restrict the type locality of *E. capito;* clearly the published designation of eastern United States is in error, and China probably embraces the lizard's actual origin, but the final fixation remains in the hands of future workers.

In like fashion we are reluctant to suggest that the name *Eumeces capito* be suppressed in order to preserve the name *Eumeces xanthi* despite the facts that (1) *E. xanthi* has been used for 85 years whereas (2) *E. capito* has never been used, except for its types, since it was proposed 95 years ago. Even *E. xanthi* was not clearly fixed with a recognizable species until 1936, however, when Taylor demonstrated that it is the same as the more familiar (even though more recently described) *Eumeces pekinensis* Stejneger (1924). Present decisions are not limited any longer by a rigid (and ambiguous) *nomen oblitum* rule. That rule is replaced by this statement: "A zoologist who considers that the application of the law of Priority would in his judgment disturb stability or universality or cause confusion is to maintain existing usage and must refer the case to the Commission for a decision under the Plenary Powers." It is to be noted that the requirement to justify suspension of the Law of Priority—use of *xanthi* by at least five different authors in at least 10 publications after Taylor's 1936 fixation—would be difficult to meet (see ICZN, 1972: 185-186). Convinced that stability of nomenclature is not a factor to be considered in the present context, we recommend that *E. xanthi* be replaced as a species name by its senior synonym *E. capito*, recognizing that it is quite likely that the name *E. xanthi* may well be utilized in the future for a subspecies of *E. capito.* Since *E. capito* is the earliest name applied to any member of the subgroup characterized by enlarged postfemorals, we

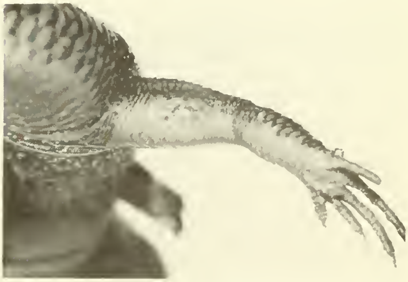

Fig. 4. Posterior view of hind leg of the holotype of *Eumeces capito* Bocourt, showing the patch of enlarged scales on thigh.

suggest that it be designated the *capito* subgroup.

Our conclusion not to recommend suppression is reinforced to a certain extent by realization that the failure of recognition of the identity of *E. capito* for almost a hundred years is not to be attributed wholly to Bocourt, for his description is exemplary in detail and illustration (even though the critical postfemoral scale character was not noted) and appeared in a widely known work. The erroneous locality was, of course, the misleading factor, but certainly not a unique one; many species have been properly allocated despite totally misleading type localities. A succession of extraordinary circumstances that prevented subsequent workers from reexamining the holotype is responsible for the name's long history as a *nomen dubium*. Had the name been proposed with a totally inadequate description or in a very obscure outlet only recently discovered, it might be construed as appropriate that it remain in oblivion; but under the circumstances as they actually exist, it is fully appropriate that Bocourt's name be given its impartial place in nomenclature, subject only to the automatic provisions of the Code. The present deficiency of an effective type locality can readily be remedied at the appropriate time, when an arbitrary designation can be proposed in conformance with detailed knowledge of geographic variation that is now lacking.

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STUDIES IN NEARCTIC DESERT SAND DUNE ORTHOPTERA. PART XV. EREMOGEOGRAPHY OF *SPANIACRIS* WITH BIOECOLOGICAL NOTES

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ABSTRACT.— Four decades of the author's records indicate that *Spaniacris deserticola* (Bruner) is confined within the periphery of the Colorado Desert. It is usually found, near or within a few hundred feet of sea level, marking the shore line of ancient Lake Cahuilla (except for the Dale Lake record). The preferred host plant is *Coldenia palmeri* growing on the lower fringes of bajadas, with *C. plicata* on drift sand being second in preference. *Spaniacris* can tolerate sand and rock temperatures of 60 C. (believed to be a maximum for Colorado Desert life). Mating takes place at that and lower temperatures. When they are disturbed while on the tops of host plants, their flight is low and direct and of short duration, and they come to rest on the torrid soil for long periods of time. The female, much larger than the male, can sustain the male in flight while mating. The study verified spatial longevity of *Spaniacris* at Indio, California, after approximately 70 years and for the Kane Springs area after 52 years.

Spaniacris deserticola (Bruner, 1906), one of the rarest of Nearctic Desert grasshoppers, was based on a single female collected at Indio by H.F. Wickham.

In 1931, Morgan Hebard (1937:376) instructed me to make special efforts to locate *S. deserticola*. Late in the afternoon of 25 August 1931, a large colony was located on a low sand ridge some ten miles east of Coyote Wells and about a mile or so east of Plaster City, California. A torrid day had been spent hunting for the elusive creature on the blistering mesas. One had to blink constantly to keep one's eyes somewhat moist, and it was so hot that the ubiquitous grasshopper *Trimerotropis p. pallidipennis* flew from the top of one creosote bush to another. At 8:00 that night, after sundown, it was still 122 F in El Centro. Hebard records that I collected 13 males and 7 females for him that day and that my brother collected 12 males and 9 females for me. In 1940 the colony was still there, and on 14 August I took 8 males and 10 females. In May 1961 I could not find any trace of the colony. During those intervening years the Highway Department had made a barrow pit out of the sand ridge and had destroyed the habitat.

During the period 1949-1973 I took 2 males and 1 female in early June 1953 at or near the mouth of Palm Canyon at a location northward and across Highway 111 from the Smoke Tree Ranch (both locations had disappeared by 1972 due to residential developments) and P. H. Timberlake took a female here on 24 June 1952 and a male on 21 June 1953.

On 22 May 1954, Dr. John Goodman and I were collecting on the east side of dry Dale Lake, 25 miles east of Twenty Nine Palms and found a female nymph, probably in the last stadium, on barren playa, where sand drifted across the gravel road. In May 1973 inspection showed this area so blasted and eroded by violent sand storms, that the only surviving vegetation was some ancient, dying creosotes with their crowns supported, like mangroves, on long exposed roots. It is believed that this colony has been exterminated. It was the only one at a considerable elevation, as all others lie close to sea level.

On 14 June 1964, I examined a rather level sweep of sand (air temperature 119 F) well covered with sand mat (*Coldenia plicata*) some miles west of Rice, California, and one several miles east of the turnoff to the Iron Mountain Pumping Station. The first plant examined contained a female *Spaniacris* quietly resting among the leaves not more than several inches above the torrid sands.

On 21 June 1964, along the old highway about 4 miles west of Thousand Palms, I found a single male. On 29 July 1974 I reexamined this area with sand mat margining the south edge of the road and scattered on the sand but could find no *Spaniacris*, although that week I had located six new colonies some miles east of Thousand Palms.

On 29 June 1970 Jim Davis took a pair of *Spaniacris* in Thousand Palms Canyon. The next day I found *Spaniacris* at that locality confined to *Coldenia palmeri* bushes bordering several hundreds of feet of an old gravel road near the base of the gravelly hills. I took 2 females and one male. Associated were: *Anconia integra* on *Atriplex canescens* var. *linearis* and *A. polycarpa; Xeracris minimus* on sandpaper weed (*Petalonyx thurberi*); *Cibolacris parviceps* on the road and *Tytthotyle maculata*, the Malpais lubber, nearby among the boulders of the brief bajada at the foot of the hills. One male was taken there 1 July 1971, and one male and one female on 3 July 1972; there were no *Spaniacris* there in 1973, a very dry year. In 1974 this area was designated Colony No. 6. (I shall report on Colony No. 6 later.)

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On the hot evening of 11 June 1973, Jim Davis and I made a night collecting trip along the roads to the Borrego Desert. One female *Spaniacris* was taken on the road 6 miles west of Salton City, just east of the radar tower; one pair was taken one mile west of the tower; and one crushed female was taken two miles west. In the arroyo area of a broad Pleistocene valley, about 13.5 miles southeast of Borrego Springs by road and within half a mile of Highway 78, another female was found on the paved road at night. In the late evening of 10 Aug. 1974, I surveyed the adjacent arroyo area, both sides of the road, but found no evidence of *Spaniacris*. The Borrego area, based on the parched conditions and poor showing of flowers, apparently got little of the daylong drizzle that drenched Coachella Valley on 7 Jan. 1974.

Theodore J. Cohn contributed some of his collection records as follows: "Imperial Co., Ca., 3 mi. E Plaster City, at the Oyster Beds Turnoff, 25 June 1965, T. J. Cohn, 1 male, 2 females. On ground near road around noon, hot as a firecracker. I have stopped there many times since and have never seen them again. Lots of *Anconia* around in other years.

"Sonora, Mexico, 22.3 mi. SE San Luis Rio Colorado, 20 June 1965, T. J. Cohn, No. 25. Base of sand dunes but not in them. 1 juv. female, last instar. *Xeracris* and *Coniana* also found here. These are the first set of dunes east of San Luis.

"Sonora, Mexico, 76 mi. SE San Luis Rio Colorado (14 mi NW Los Vidrios), 14 June 1966, T. J. Cohn, No. 16. Very sparse vegetation on moderately sandy soil, not far from stabilized dunes. This was around a corral a few hundred yards south of the road, near the next set of dunes, 1 female. Lots of what I think is *Coniana* here."

The sand dunes 22.3 miles SE San Luis are in large part in Arizona; the International fence terminating on some rocky hills astride the International Boundary. The best dunes are in Arizona immediately north of these hills. I have collected there on many occasions but have never found evidence of *Spaniacris*. This should be the best location to discover *Spaniacris* in Arizona. At the 76-mile location, a high ridge of aeolian dunes sweeps far inland into the area from the southwestern coastal regions.

Notes on the 1974 Survey

Colony No. 1. Found, 25 July 3 miles north of Indio, California, on Monroe Street on *C. palmeri* on the north side of the dyke protecting the Coachella Valley branch of the All American Canal within fifty feet of the paved road. The Colony was at the southern edge of a considerable bajada that gently slopes down from the Indio Hills over an area of many miles. This location is directly south of the Curtis Desert Palms Oasis, whose existence is threatened by the huge Massey Rock and Sand gravel pit. The plant life is typical of that described fully under No. 2 below but is not as extensive. Thus, the presence of *Spaniacris deserticola* for Indio was verified almost 70 years after Bruner described it in 1906; I have not been able to find the date of Wickham's collections prior to 1906.

Colony No. 2. That afternoon, at the powerline crossing of Washington Street, 4 miles north of Interstate 10 and about 10 miles northwest of Indio, I found a much larger colony, here designated No. 2. The location was similar to that of No. 1, representing the southern edge of the long bajada margining the south side of the Indio Hills. The desert vegetation consists of shrubs, living ephemerals, and the dead skeletons of spring ephemerals.

The desert shrubbery was composed of many widely scattered *Coldenia palmeri* growing along the narrow, poorly paved powerline road as well as along the margins of a shallow dry-wash with fewer scattered clumps of creosote (*Larrea divaricata*), sandpaper weed (*Petalonyx thurberi*), Burrobush (*Franseria dumosa*), and even more rarely encelia (*Encelia farinosa*), desert sweet (*Bebbia juncea*), cheesebush (*Hymenoclea salsola*) and California dalea (*Dalea californica*). Living ephemerals were: inflated stem (*Eriogonum inflatum*), Spanish needle (*Palofoxia linearis*), velvet rosette (*Psathyrotes ramosissima*), *Stillingia spinulosa*, and *Tidestroemia oblongifolia;* all but *Tidestroemia* were in bloom. Dry spring ephemerals were: desert gold (*Geraea canescens*), forget-me-nots (*Cryptantha costata* and *maritima*), Thomas buckwheat (*Eriogonum Thomasi*), brown-eyed primrose (*Oenothera clavaeformis*), blazing star (*Mentzelia multiflora*), and perhaps others. The presence of the flowering ephemerals in July and August on the blazing Colorado Desert can be explained only by the slow drizzling rain (1.56 inches) on 7 Jan. 1974, which penetrated to at least three feet. On 29 July, I found damp sand one foot down. Although this soil moisture was a great boon in reviving dying shrubs (transects anywhere will show 65-75 percent dead or partly dead), germination of ephemeral seeds was poor because of the cold January weather. The deep penetration of moisture accounts for the flowering of *Palofoxia* and *Eriogonum* in midsummer and undoubtedly was responsible for breaking the diapause of *Spaniacris* and other acridid eggs.

On 25 July the two-acre area surveyed (approx. 100 by 80 yds.) contained at least 6 pairs of *Spaniacris* of which I took 3 males and 2 females, leaving the rest for propagation. Next day, 26 July, 4:15 to 5:00 pm, slightly hazy, temperature 45 C, soil 57 C. Quite a few adults noted but none taken.

On 17 Aug. a hot wind was blowing from the southeast. At 5:00 pm, air temperature was 44 C, soil 54 C; 5:20 pm, air 44 C, soil 53 C. Photographed *Spaniacris* with Tri-X film. Found *Coniana snowi* and for the first time *Anconia integra* female on *Coldenia palmeri*. *Xeracris minimus* also sometimes found but more often taken from *Petalonyx thurberi*.

On 20 Aug. 5:00 to 6:30 pm, air 38 C, soil 54 C. Found only a few pairs in the original two-acre area. Extended the colony southeastward for 3/10 mile, where I found two pairs, and westward across Washington Street at least 100 yards, where I found two more pairs, one pair in copula, at 6:30 pm. Total area covered by Colony No. 2, at least one half mile in length and about 100 yards in width. Photographed the species with Panatomic-X film as Tri-X was much too fast for glaring light of the desert.

On 24 Aug. 5:30 to 6:30 pm visited the site with Chas. Neeley, photographer. At 5:30 pm, air 41 C, soil 51 C. First male found within a few feet of the road. One area four feet square formed by two contiguous *C. palmeri* plants held two females and one pair mating; this is the greatest concentration ever found for this species. On this date the original two-acre area contained eight females and nine males despite the fact that three males and two females were removed on 25 July. Since that date all specimens left for propagation of the species. Little change in vegetation noted since 25 July. Fairly hot, slight breeze from the west.

On 18 Sept., 1:15 to 2:00 pm, air 41 C, soil 51 C. One male found near road, one female at least 200 feet away. This female recognized by the slightly shorter tegmina. *Trimerotropis p. pallidipennis* present for the first time this summer; four females noted. These had probably migrated into the area as no nymphs of any acridids had been noted previously.

On 29 Sept., 1:15 to 2:00 pm, fairly hot wind, temperature: air 39.5 C, soil 52 C. Examined all *C. palmeri* bushes in the original two-acre area. On the 91st plant the female noted on 18 Sept. was found and some distance away on the 104th plant found a pair, in copula, missed on 18 Sept. Did not find the male found 18 Sept. near the road, which had been at least 200 feet away from the others. It is obvious that *Spaniacris* is quite localized in its movements especially in the late summer.

On 4 Oct., brisk west wind, air 31.5 C, soil 54 C on sunny side of a *C. palmeri* plant in wind-sheltered position. Examined about 120 plants; apparently only one female surviving at this late date; this one, the one noted on 18 and 29 Sept., was still in the same area. I found female by waving my net back and forth near each plant. While doing so, I was aware of the slightest movement of something dropping an inch or two from the end of a branch to the ground. This female was hiding under the plant on the sandy soil. This was the first time I had observed this habit and the first record of this species for October.

On 11 Oct., 11:20 to 11:40 am, much cooler. Had time only to check over those bushes mostly likely to hold *Spaniacris* perched on top of plant as they almost always were. Found none; believe colony had died out for 1974. On this late date vegetation was surprisingly like that noted in late July, with *E. inflatum*, *Palofoxia linearis*, and *P. ramosissima* still blooming, but *Stillingia* has been dead and brown since mid-September.

Colony No. 3. Located 25 July, about one mile northwest of Colony No. 2, on the south side of Washington Street as it swings west to join the east end of Ramon Road at the turnoff to Thousand Palms Canyon. The colony comprised about 600 yards of *C. palmeri* on the east and west slopes of a gentle hill with a few plants of *Dalea californica* and *D. emoryi* here and there. The road crosses the south marginal area of the Indio Hill's bajada. The 300 yards of the east slope contained at least five pairs of *Spaniacris;* one pair taken; west slope at least two pairs; one pair taken. When disturbed this species never flies to another *C. palmeri* bush but always alights on the very hot soil. Flight is low and direct, the wings showing rather deep azure. On the food plant it usually orients the long axis of its body parallel to the rays of the sun so that usally only the face is exposed to the full effect of the very hot sun. Under the circumstances this reduces exposure to the minimum, and the very long legs help elevate the body from the extremely hot soil tempartures. *Spaniacris* is not wary: the cautious photographer can move the macrolens of his camera to within 8 inches of the grasshopper. *Trimerotropus p. pallidipennis* seldom permits approach closer than 10 feet.

Colony No. 4. Found 29 July, located just east of the Thousand Palms Canyon Turnoff. About one-fifth of an acre of *C. palmeri* fairly widely scattered with a few creosote interspersed; 2:30 pm, air 37 C; (had been overcast in am), soil 58 C. This small area (100 x 100 ft) revealed at least 9 females and 11 males, some of which were on very hot ground. Most of the females were on the plants. While I was taking temperature readings, one pair, in copula, sat on a rock (58 C) for at least five minutes without showing any signs—as other acridids quickly do—that the rock was hot. Evidence seems to indicate that *Spaniacris* can tolerate more heat than can any other animal living on the torrid Colorado Desert. Temperature one foot above soil level was 45 C. Still on margin of the bajada.

Colony No. 5. Found 25 July, one half mile west of Turnoff to Thousand Palms Canyon, 4:30 to 5:00 pm, air 45 C, soil 55 C. Margin of the same bajada but sandier than in previous colonies. Flora: *C. palmeri* with scattered creosote, *D. californica*, cheesebush, *Dicoria canescens*, *Atriplex c. linearis*, and dead sand verbena (*Abronia villosa*). One pair in copula, female could fly only a few feet with the male. Took mating pair and left 2 males and one female.

Colony No. 6. Visited once on 25 July. This is the location mentioned previously under dates of 1970-1973, within the mouth of Thousand Palms Canyon. Observed 1 female and 1 male perched on *C. palmeri* along margin of old gravel road previously described. Did not disturb. Noted *Anconia integra* on *Atriplex c. linearis*, *Xeracris minimus*, and flushed a female *Tytthotyle maculata* out of luxuriant creosote bush. No temperature readings were made on the first day of 1974 survey.

On Saturday afternoon, 27 July, I continued my *Spaniacris* survey. Driving northward on Washington Street and then westward, I passed colonies 2, 3, and 4, then turned right on Thousand Palms Canyon Road to pass Colony 6 and reach the Dillon Road junction in about four and one-half miles. En route I examined 400 yards of fine habitat of *C. palmeri* on both sides of the road about 1.5 miles north of Paul Wilhelm's Oasis, but found no specimens. As this was about as fine a habitat as I had seen, I wondered why no *Spaniacris*. Apparently, since it is so rare, localized, and sedentary in habits and because this location is several hundred feet higher than Colony 6, it has not been able to penetrate up through this rather broad and low canyon.

A survey of Dillon Road from the Thousand Palms Canyon junction (approximately 600 feet elevation) southeasterly 11 miles to where sand is first encountered at about sea level, revealed no *Spaniacris*.

Colony No. 7. Shortly beyond, at 11.7

miles from the Dillon-Thousand Palm Canyon junction, I examined 200 yards of *C. plicata* and found on one plant one male *Spaniacris* and 1 female *Coniana snowi* resting on top of the low bush within one foot of each other. Air temperature at 6:00 pm, 45 C with hot wind blowing, 44 C when calm, leaf surface 44.2 C. This location was 3.6 miles northwest of freeway and about 5 miles northwest of Coachella.

Both sides of Dillon Road, edged with sparse patches of *Coldenia palmeri* and *C. plicata*, were examined from Colony No. 7 to the junction with Interstate 10 (3.4 miles) and no *Spaniacris* were found.

On 29 July, I examined old Highway 99(now Varner Road) from Thousand Palms west to Garnet Hill (13.3 miles) and found no trace of *Spaniacris* on *Coldenia palmeri* and *C. plicata*, which often formed nice colonies along the margin of the road.

On 10 Aug. I drove along Highway 86 to the Kane Springs area, then westward on Highway 78, but failed to find evidence of *Spaniacris* other than at Colony No. 8, noted below.

Colony No. 8. At about 7.5 miles from Kane Springs, 6 miles northwest of the junctions of Highways 78 and 86, I examined 100 yards of *C. plicata* growing on south sandy side of the road and found a female *Spaniacris* that flew about 30 feet, its azure wings showing in low direct flight, to land on the bare clay soil typical of the area. Later I examined a small flat wash with *C. plicata*, creosote, and smoke tree (*Dalea spinosa*) about six miles northwest of Kane Springs that admirably fits Hebard's (1937:377) location where he took this species. Nothing was found here.

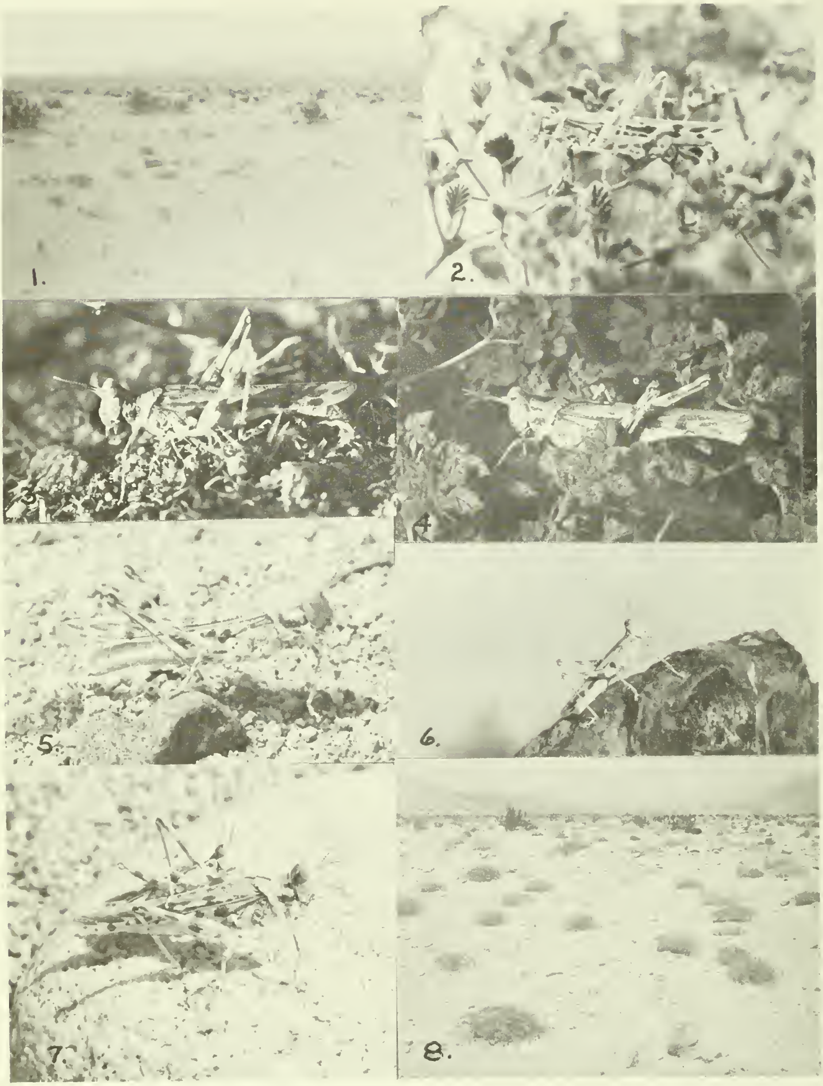
Because of drought conditions there was very little *Coldenia* west on Highway 78 and what there was occurred chiefly at the sea level line some 6 to 7 miles west of the Kane Springs junction. Late that night, at about 10:30 pm, I examined by Coleman lantern light the area immediately east of the radar tower where *Spaniacris* had been encountered on the night of 11 June 1973, but found nothing. I had examined about 10 acres of this area in late afternoon of 20 July 1974; but, although it was in interesting habitat, I could find no *Spaniacris*. Farther on, 4 miles west of Salton City, I examined 300 yards of roadside *Coldenia plicata* with Coleman lantern and found nothing but *Coniana snowi*. I had also examined this area on July 20.

Summary and Conclusions

Biology. The adult *Spaniacris* is now known from early June until early October. Records of nymphs in May represent the two last nymphal stadia. No small nymphs have ever been found. The number of ova laid per female is small, so the population potential is likewise small.

Habits. The low direct flight of rather short duration is diagnostic for the genus. During flight the wings appear darker azure than they appear on close inspection. Flight is almost always from the top of the *Coldenia* plants to the desert soil, where they will rest immovable many minutes, seemingly able to tolerate perfectly the torrid soil temperatures. *Spaniacris* is not a wary grasshopper and can be slowly and easily approached to within six inches for macrolens photography. However, quick lateral movements will alarm them and cause flight. The female of this species is probably the only grasshopper that can sustain flight, carrying the male, while mating. I never failed to find mating pairs in the larger colonies during afternoon and late evening hours. No observations were made in the early morning. Mating was observed from late July to late September. Oviposition was not observed. During the hotter portions of the day, from late morning until late evening, females oriented themselves so that the long axis of the body was parallel to the rays of the sun. In such positions only the front of the long face was exposed to the full effect of the rays. Only on rare occasions, and that in the late evening, did I observe males and females resting on the shady side of their host plant (Fig. 4).

Habitat. The marginal fringes of great bajadas, where the soil is partly of rock, sand, and clay, seem to be the preferred habitat. *Spaniacris* has been taken in purely drift sand locations near Rice (Figs. 1 and 2), Dale Lake, and the northwestern Sonora, Mexico (records of Dr. Cohn). The preferred altitudinal habitat appears to be at or slightly above the sea level contour line in the Colorado Desert; no captures have been made below sea



Figs. 1-8. Habit and habitat photographs of *Spaniacris deserticola*: 1, Habitat of drift sand, with *C. plicata in foreground, some miles west* of Rice, Ca., 14 June 1964, 119 F in shade; 2, Female resting in top of *C. plicata* at Fig. 1 locality; 3, Female (by Chas C. Neeley), 24 Aug. 1974, late evening at Colony No. 2; 4, Female resting on *C. palmeri* in shade of setting sun, Colony No. 4, 29 July 1974, taken with Vivitar Strobe Flash No. 292 with white cloth filter; 5, Female on hot gravelly soil, Colony No. 2, 20 Aug. 1974, soil surface 54 C; 6, Male, Colony No. 6, 30 June 1970; 7, Mating pair, Colony No. 4, 29 July 1974, resting on rock surface, 58 C, 2:15 pm; 8, Habitat, Colony No. 4, *C. palmeri* in foreground; some Creosote in background, looking north up Thousand Palms Canyon, 29 July 1974, 2:30 pm. All photographs taken by Ernest R. Tinkham except No. 3, which is by Chas. C. Neeley.

level. The only records of considerable elevation (± 1000 feet) appear to be the captures at Dale Lake and near Rice. There are no records for sand dune situations. Thus, the sea level contour represents the ancient shore line of Pleistocene fresh water Lake Cahuilla, which dried up hundreds of years ago to leave the salt deposits of the Salton sea depression before flooding in 1903. It is obvious, because *Spaniacris* is still largely confined to the old beach line, that its powers of dissemination must be rather poor. This seems partly accounted for by its sedentary habits (as noted under Colony No. 6), by its low egg potential, by the restricted habitat of its chief host plant (*C. palmeri*), by the torrid temperatures, by the great aridity of its habitat, and, perhaps, by other factors as well.

Host Plants. *Spaniacris* appears to be strictly confined to *Coldenia palmeri* and *C. plicata*. The Palmer coldenia seems to be the preferred host because its distribution is closely related to the sea-level beach line of ancient lake. Other factors in the choice of host plants appear to be the size and greater height of *C. Palmeri*, which provides green foliage all summer long, and the edaphic conditions which provide greater protection than the sand (inhabited by *C. plicata*) for the eggs during drought-induced diapauses. Very little is known about the diapause in the eggs of desert acridids. On the other hand, sand appears to be a poor medium for the protection of eggs, especially if laid close to the sand surface.

Temperature Tolerance. *Spaniacris* appears to tolerate torrid soil and rock temperatures of 140 F (60 C), as portrayed by the mating pair in Photo 7, without exhibiting any of the signs of intolerance (such as the lifting of tarsi) that most other desert acridids would soon portray under such situations. Its extremely long legs (for an acridid) must be partly responsible for this heat tolerance. Thus, the evidence seems to indicate that *Spaniacris* can tolerate higher temperatures than any other life form associated with the Colorado, our hottest desert.

Spatial Longevity. The evidence provided by Colonies 1 and 8 indicates that *Spaniacris* has survived in the Indio area for 75 years, and in the location a few miles northwest of Kane Springs for 50 years, which is more than half the time of American occupation of the territory. However, in the areas near Dale Lake and Palm Springs and west of Thousand Palms there is evidence that the destructive practices of man have extirpated three colonies of *Spaniacris* within the past two decades. These practices include scraping off large areas of desert shrubbery, asphalt paving of huge areas, and many other methods well known to conservationists, all of which helped produce the increasing droughts and sandstorms of the past two decades. It is also apparent that *Spaniacris* survived many millennia in the Colorado Desert before the advent of the white man.

Faunal Designation. *Spaniacris* appears strictly confined to the Colorado Desert, its zonal distribution being confined largely to the old beach line of Pleistocene Lake Cahuilla, which is also at sea level.

Orthopteran Associates. The chief associates are: *Coniana snowi* especially on sandier habitats dominated by *C. plicata; Xeracris minimus*, showing a preference for *Petalonyx thurberi;* and, rarely, the saltbush grasshopper (*Anconia integra*), which prefers *Atriplex* spp. Also present are soil-dwelling species such as the Arroyo Grasshopper (*Cibolacris parviceps*), the ubiquitous *Trimerotropis p. pallidipennis*, rarely the Malpais lubber (*Tytthotyle maculata*) as in Colony 6, and the ground mantid (*Litaneutria minor*).

Enemies. Since the 1974 survey demonstrated that many colonies exist along road margins favored by *C. palmeri* and (where sandier) *C. plicata*, evidence indicates that many *Spaniacris* are crushed by passing cars, especially at night, when there seems to be considerable nocturnal activity among desert acridids. As the crested lizard is strictly herbivorous, there seems to be no evidence that it would feed on *Spaniacris;* but the presence of zebratails and, rarely, sand dune lizards of the genus *Uma* in sandy habitats where *C. plicata* is growing may pose a threat to the early stages of *Spaniacris*, about which nothing is known.

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ROOSTING BEHAVIOR OF MALE *EUDERMA MACULATUM* FROM UTAH

Richard M. Poche[1] and George A. Ruffner[2]

ABSTRACT.— Eight spotted bats (*Euderma maculatum*) were captured and released along the Fort Pierce Wash, Washington County, Utah, in August 1974. Observations indicated that *Euderma* roosts in cracks and crevices.

According to Easterla (1970, 1973), the spotted bat (*Euderma maculatum*) probably utilizes cracks and crevices as roosting sites in Big Bend National Park, Texas. Observations by Poche (1974) indicate that the spotted bat inhabits similar daytime retreats in Utah.

Between 12 and 15 August 1974, eight spotted bats were netted over Fort Pierce Wash, Utah. All were sexed and marked using a wing perforating numbering system. Only one female (apparently postpartum) was obtained, and six of the seven males captured were scrotal.

The mean weight for spotted bats captured was 13.9 g, with a range of 14.8 to 13.6 g. After marking, the bats were released individually, and the path of flight was followed with binoculars. The first individual set free on 13 August disappeared into a narrow crack along the steep-walled canyon. Esterla (1973) reported similar postrelease behavior in Big Bend National Park.

A second *Euderma* flew west of the Fort Pierce ruins when released and landed on the near-vertical walls of the Navajo sandstone cliffs, whereupon the bat walked about easily in search of a crevice. Easterla (1972) and Parker (1952) previously reported *Euderma* walking over horizontal surfaces; but the bat that we released searched over the vertical wall with great facility. J. S. Findley (pers. comm.) reported similar observations of captive spotted bats walking over volcanic rocks which, however, are more porous than sandstone. As the second bat climbed the wall, it appeared to use its ears as probes in searching for a crevice. After approximately two minutes of crawling about, the bat crept into a narrow crack about 3 cm wide.

A third spotted bat, when released on 14 August, flew south of the wash and went out of view behind a large boulder. After five minutes of searching, we located the animal beneath a rock about 50 cm in diameter. It apparently had backed underneath the fallen rock. The bat was well concealed and ordinarily would not have been noticed.

The fourth bat we released flew under a large boulder on the side of a steep incline. It was found hanging by its feet at a 15 degree angle on the side of the rock.

The fifth bat, liberated on 14 August, flew north of the wash and up the steep slopes. This animal landed on the face of the cliff, and like the second individual, it engaged in seeking out a crack into which it could withdraw. Because of the observation distance, it was impossible to detect which crack the bat selected. We climbed the cliff and in fifteen minutes located the *Euderma*. The bat had moved into a narrow angling fracture and was detected by blowing into the crack. This procedure produced a loud clicking sound by the bat, typical for the species when disturbed.

On 15 August 1974, a sixth spotted bat (female) was netted, and numerous ectoparasites were noted. The bat escaped from the holding bag while on the hood of our truck. Another male collected the same morning hosted numerous mites. These were later identified as *Cryptonyssus desultorious*, and this was the first report of an ectoparasite associated with the spotted bat (Radovsky and Poche, 1975). The male also had a large (3 to 5 mm) swollen infection on the right forearm, near the elbow. This individual was released at 2000 hours at Fort Pierce, and it flew approximately 30 m down the north side of the wash and landed in a depression on Navajo sandstone. It immediately climbed about the near-vertical cliff face, looking for a crevice. As expected, the pollex appeared to serve as the main tool for grasping.

After several unsuccessful attempts to locate a crack large enough to crawl into, the *Euderma* appeared to be "nervous."

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While we were attempting to photograph the bat, it flew from the wall to a ledge with an overhang of 3 meters. At this time, we abandoned pursuit rather than harass the bat any further.

Poche and Baillie (1974) and Poche (1975) reported observations indicating that the natural roost of the spotted bat in the Utah-Arizona region is small cracks and crevices. The findings presented here lend evidence to the validity of these earlier notions. The fact that three bats were observed in active search for factures while they were suspended almost vertically, further supports the suggestion.

We wish to express our thanks to the Nevada Power Company for financing this study. C. E. Baker and D. J. Schmidly provided helpful comments in reviewing the original draft.

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THE NEST AND LARVA OF *DIPLOPLECTRON BRUNNEIPES* (CRESSON) (HYMENOPTERA: SPHECIDAE)

Howard E. Evans[1]

Abstract.— *Diploplectron brunneipes* (Cresson) makes a shallow nest in compact clay-sand containing at least two cells. It is provisioned with immature Heteroptera. The larva resembles that of *Astata* in a general way but differs in several particulars.

Wasps of the genus *Diploplectron* escape frequent detection because of their small size (4-7 mm) and secretive behavior. For many years the genus was poorly understood, but in 1972 there appeared two important papers: Parker presented a revision of the 15 New World species, with notes on the biology of 4 of them; and Kurczewski published a fairly detailed study of the nesting behavior of one of these (*D. peglowi* Krombein). The present paper includes brief observations on a previously unstudied species, *D. brunneipes* (Cresson), as well as the first description of a larva of this genus. The latter is of some importance, as knowledge of the larvae of this subfamily (Astatinae) has previously been based only on the genus *Astata*, and there are some discrepancies in the published information on that genus.

These observations were made along the shores of Terry Lake, just north of the city of Fort Collins, Colorado. *D. brunneipes* was not uncommon during July and August 1974, especially in strips of bare, flat soil on top of a bank bordering the beach proper. A number of females were seen walking and flying about low vegetation, apparently hunting. Only one nest was found. This was located in the center of a bare strip of rather hard-packed sandy clay. On 24 July a female was seen walking in a circuitous path holding a small bug in her mandibles. After a few moments she plunged into a small, open hole having a diameter of 2.5 mm and having no evidence of a mound of soil around it.

The female was captured when she emerged from this hole a few minutes later. The burrow was found to penetrate the soil at about a 60 degree angle with the surface. Two cells were located, at depths of 5.5 and 6.5 cm, the two cells being 4 cm apart and about 9 cm from the entrance. Each cell contained 6 immature bugs, *Uhleriola floralis* (Uhler) (Lygaeidae) [det. J. A. Slater] and a small larva, one of which was reared to maturity and is described below. Both of these cells had been closed off with a barrier of sand. Since the wasp had just brought in prey, there must have been a cell in the course of being provisioned (or prey stored in the burrow), but this was not found. The cells were broadly elliptical, measuring about 3 x 4 mm. The bugs, all approximately the same instar, were in some cases on their backs, in other cases on their sides.

Description of Larva

Length (measured in usual curved position) 6.2 mm; maximum width 2.3 mm; maximum height (4th abdominal segment) 2.4 mm. Body fusiform, middle segments somewhat humped dorsally, 4th abdominal segment more humped than any other; anus terminal and supraanal and subanal lobes equally developed (Fig. 2). Pleural lobes rather weakly developed; division of segments into dorsal annulets indistinct posterior to middle of body. Integument smooth and glistening, under high power seen to have a very few minute setae, chiefly on the dorsum and pleural lobes of the more anterior segments, also sparse, minute spinules on parts of the venter and pleura. First pair of spiracles slightly larger than the others; atrium somewhat pear shaped, sparsely lined with anastomosing ridges; peritreme distinct; opening into subatrium simple, unarmed (Fig. 5).

Head 0.9 mm wide, 0.7 mm high (exclusive of labrum) (Fig. 1). Head largely unpigmented, except mandibles and pleurostomal thickenings brownish; center of front with paired, small depressions; parietal bands very weak. Antennal orbits elliptical, papillae only slightly longer than wide at base. Head with only a very few

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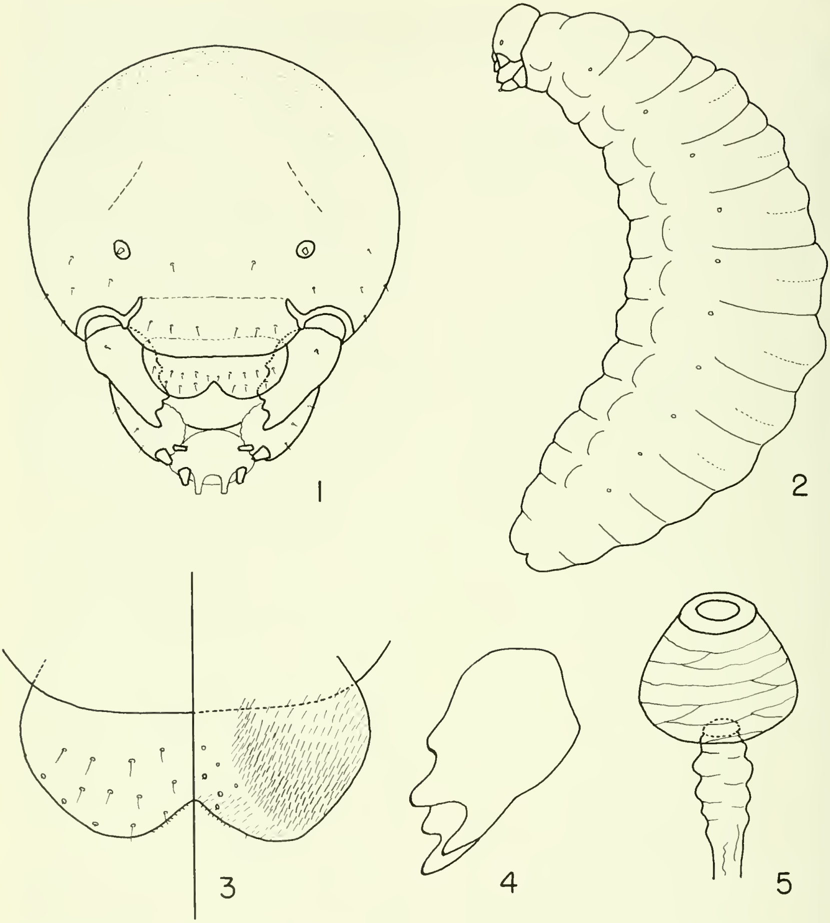

Figs. 1-5. *Diploplectron brunneipes*, mature larva: 1, head; 2, body, lateral view; 3, labrum (left side) and epipharynx (right side); 4, mandible, ventral (posterior) aspect; 5, anterior thoracic spiracle, high magnification.

small setae. Labrum 0.33 mm wide, with a strong V-shaped median emargination; surface with about 20 small setae, also with a few small marginal sensilla, mainly laterally; epipharynx with 6 strong sensillae surrounding the emargination and some weaker ones basal of these, otherwise clothed with very fine spinules except medially (Fig. 3). Mandibles stout, with 5 strong teeth, one of them ventral of the most apical tooth (Fig. 4); upper surface with a single minute seta. Maxillae short, directed mesad, inner surface roughened but not distinctly spinulose; galeae very much more slender than palpi. Hypopharynx inconspicuous and evidently not spinulose. Labium without setae or spinules, spinnerets blunt, considerably exceeding the palpi.

Discussion

The nest of *D. brunneipes* closely resembles that of *D. peglowi* Krombein, as described by Parker (1972) and Kurczewski (1972), although evidently in flatter and more compact soil than that species usually occupies. The angle of the burrow, depth and size of the cells, and open nest entrance are similar in the two species, as are the type of prey and manner of prey carriage.

The larva is basically similar in structure to that of *Astata* as described by Evans (1958), although differing in some details from descriptions provided by earlier workers. The paired spinnerets, humped fourth abdominal segment, terminal anus, short antennal papillae, stout mandibles, mesally directed maxillae, and smooth integument together clearly define the Astatinae as distinct from other subfamilies. One other feature that I used to define the subfamily, the presence of numerous setae on the mandibles, does not hold up, and it represents an important difference between the larvae of *Astata* and *Diploplectron*. Other differences include the 5-toothed mandibles of *Diploplectron*, the sparser head setae, and the lack of conspicuous labral sensory cones.

The larva of *Astata* feeds in an inverted position in the cell, the egg having been laid on the ventral side of a bug placed with its dorsum upward in the bottom of the cell (Evans, 1957). I had assumed that the humped 4th abdominal segment represented a pseudopod that assisted the larva in feeding in this unusual position. However, the species of *Diploplectron* place the bugs in the cell in various positions, and according to Kurczewski (1972) the bug bearing the egg is found either on its side or with its venter upward. Of course the middorsal hump may still serve to assist the larva in pushing itself about from prey to prey, though it seems less suitably adapted for this type of feeding.

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The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

VOLUME 35 June 30, 1975 No. 2

A REVISION OF THE *PHACELIA* CRENULATAE GROUP (*HYDROPHYLLACEAE*) FOR NORTH AMERICA

N. Duane Atwood[1]

ABSTRACT.— This taxonomic monograph of the *Phacelia* crenulatae group for North America recognizes 35 species and 7 varieties. A brief discussion of the history, general morphology, phylogeny, and cytology is given. All entities are separated by a comprehensive key, followed by a list of types, synonyms, descriptions, and general habitat. Distribution maps and illustrations are included. One variety is described as new. The body of this work is based on herbarium specimens and extensive field observations and collections made throughout much of North America.

INTRODUCTION

The Crenulatae group of *Phacelia* belongs to the subgenus Phacelia, section Phacelia, and may be distinguished from other members of the section by the four-seeded capsule and excavated ventral surface of the seeds. Many of the species are viscid and ill-scented desert plants confined mostly to western North America and Mexico. The remaining species occur in South America and in the midwestern and the west central parts of the United States.

The lack of phenologic, edaphic, morphologic, and distributional data plus the description of additional species since the monograph by Voss (1937) have necessitated a thorough study of the group. Very little was known about the species occurring in Texas, New Mexico, Arizona, Utah, and California or species in Mexico and South America. Previous revisions were based entirely on herbarium specimens, and, possibly because of this fact, numerous errors and misconceptions appeared in them. Therefore it became necessary to conduct extensive field work wherein most of the entities were examined in living condition.

Phacelia integrifolia Torr. was the first species of the Crenulatae group to be described. It was collected by James in June 1820 but was not described until 1826. The next taxon was described in 1835 when Hooker named *P. congesta* from plants collected by Drummond in the vicinity of Galveston Bay, Galveston County, Texas. In 1848 Nuttall described *P. glandulosa* from specimens collected the same year, "about Ham's Fork Colorado of the West." Hooker (1851) assigned *P. glandulosa* to the genus *Eutoca*. Since 1849, 41 nominate species have been described. Of the 78 names proposed in this group, fewer than half of them are recognized as valid taxa in the present study.

MATERIALS AND METHODS

Research materials for this study have come from two major sources: a large quantity of plants borrowed from herbaria in Germany, Mexico, and the United States, and from field studies made during the growing season of 1968 in Utah, Arizona, and Wyoming; in 1969 in Arizona, California, Colorado, Utah, and Wyoming; and during 1970-1971 in Texas, Mexico, Arizona, New Mexico, California, and Utah.

Measurements of such large plant parts as stems, leaves, and inflorescences were made with a metric ruler. Small structures such as calyces, flowers, capsules, and seeds were measured with the aid of an ocular micrometer fitted to a stereoscopic microscope. At the end of each description a list of specimens examined in the study of each entity is given. The number following the description indicates the total number of specimens seen, while the number in parentheses indicates the number of collections made by the author. The standard abbreviations of herbaria, with a few exceptions, are those of Lanjouw and Stafleu (1964). These indicate the herbaria from which specimens were examined. The type specimens examined were photographed and the photographs deposited in the herbarium at Brigham Young University; they are indicated by an exclamation mark following the herbarium symbol designation in the list of synonyms.

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B	Botanischer Garten and Botanisches Museum, Berlin-Dahlem, Germany
BRY	Brigham Young University, Provo, Utah
CAS	California Academy of Sciences, San Francisco, California
GH	Gray Herbarium, Harvard University, Cambridge, Massachusetts
JEPS	Jepson Herbarium, University of California, Berkeley, California
MEXU	Herbario Nacional del Instituto Biologia, Universidad Nacional de Mexico
NY	New York Botanical Garden, New York, New York
POM	Pomona College Herbarium, Claremont, California
RM	Rocky Mountain Herbarium, Laramie, Wyoming
RSA	Rancho Santa Ana Botanic Garden, Claremont, California
UC	University of California, Berkeley, California
UNM	University of New Mexico, Albuquerque, New Mexico
US	United States National Museum, Washington, D.C.
UT	University of Utah Herbarium, Salt Lake City, Utah
UTC	Intermountain Herbarium, Logan, Utah
WTS	West Texas State University, Canyon, Texas

Seeds provide important distinguishing features, and, therefore, the Electron Scanning Microscope facilities at Brigham Young University were used to photograph them. They were air-dried and mounted on polished brass specimen stubs with Elmer's glue which had been diluted one part glue to three parts water. The specimens were coated with gold (200-300 angstroms) using a rotating stage and examined with a Hitachi SSM-2 microscope. All specimens were examined with the microscope beam voltage set at 20 kv.

General Morphology

Members of the Crenulatae group are annual, biennial, or perennial herbaceous plants. They possess a simple taproot, which varies in size depending on the species and even on the individual plant. The stem pattern varies considerably between species but basically consists of an axis which is usually foliate and bears several to many scorpioid cymes. The majority of species are annuals which complete their life cycle in two to three months. However, the seeds of some species, such as *P. corrugata*, generally germinate in the fall and produce a rosette of leaves. This rosette is small at first but continues to grow during the warmer periods of the winter months. Then in the spring it produces a flowering shoot. These are winter annuals. The biennial species, as well as some annuals, generally have thick stems and produce a basal rosette of leaves. The perennial species have a thickened woody caudex which produces one to several herbaceous branched or simple stems. These are terminated by a series of scorpioid cymes.

Leaves

The leaves vary from simple to bipinnately compound, with a series of intermediate types. About half the species have simple leaves with the margins crenate to dentate, irregularly serrate, or incised. Those taxa having compound leaves are usually quite distinct from the foregoing, but variations between the two types exist. The margins of some leaves, such as those of *P. constancei*, *P. intergrifolia*, and *P. welshii*, are often revolute. A basal rosette is usually present in biennial, perennial and some robust annual species. The basal and lower cauline leaves are typically larger and longer-petiolate than the gradually reduced upper cauline leaves. Leaf pubescence varies depending on the species, but the leaves possess either one or, more often, a combination of pubescence types. In general, leaf characters have not been used to delineate species, since other less variable and more important taxonomic characters are available.

Inflorescence

Heckard (1960) indicated that agreement is generally lacking as to the exact terminology used to describe a branched system of scorpioid cymes. However, the inflorescences are generally best described as being composed of compound scorpioid cymes. In some species, such as *P. coerulea* and *P. bombycina*, the inflorescences appear to be racemose. The flower cluster is actually a false raceme because the flowers are all borne on one side of the peduncle. In most species the inflorescence is open but with terminally congested clusters. In *P. palmeri*, *P. utahensis*, and *P. vossii* the inflorescence is congested into a spicate thyrsus. The inflorescences are generally more glandular than the stems and leaves. The individual cymes of *P. integrifolia* elongate to as much as 2.1 dm in fruit.

Flower

Corolla: The flowers are crowded along a coiled peduncle that uncoils as flowering advances. The shape, size, and color of the corollas are taxonomically important. The corollas are funnelform to rotate or campanulate in shape, and blue, purple, violet or lavender in color. One series of taxa has white to lavender tubular corollas. The corolla lobes are normally entire or, at the most, merely crenulate and finely pubescent. However, in *P. neomexicana* and its relatives the lobes are either fimbrate or denticulate. The pedicels are commonly less than 3 mm long with exceptions in *P. pedicellata* and *P. scariosa*, in which the pedicels are 6 and 8 mm long respectively.

Corolla scales: Corolla scales are present in all species of this group and occur in pairs at the base of each filament. The variation in size, shape, and attachment of the scales offers some variation, but as a whole it is not as useful in delineating species as are other characters.

Androecium: The filaments are attached at the base of the corolla tube and vary in length depending on the taxa involved. Even in individual plants filament length varies considerably. The filaments are glabrous in all species. The anthers are dorsifixed, ca. 1 mm long and 0.5 mm broad, and open their full length by two longitudinal slits. The pollen has not been studied systematically. The stamens as well as the style in *P. coerulea*, *P. denticulata*, and *P. anelsonii* are included within the corolla, or nearly so. This feature has been given taxonomic importance, but it varies in some populations, as noted in *P. coerulea* and *P. denticulata*. In these instances, the stamens are barely exserted from the tube. Some confusion may occur in keying out collections of plants that are in early anthesis, since the stamens of most species are folded in the bud and become exserted only when the flower is fully opened.

Gynoecium: The gynoecium consists of an ovoid to subglobose or oblong, usually puberulent and commonly glandular ovary. The persistent bifid style is terminated by small stigmatic areas. The bifurcation of the style varies from two-thirds to three-fourths of its length, with the lower undivided portion being pubescent. The ovary is 1-celled or incompletely 2-celled by union of the placentae. Four ovules are commonly produced; however, sometimes one is reduced in size or, less frequently, lacking altogether. This condition appears only sporadically and is probably influenced by environmental and nutritional factors.

Calyx: The calyx is five-parted to the base, or nearly so. The lobes vary in size and shape from species to species. There is consistent variation in flowering and fruiting calyces with those in fruit being larger and sometimes scarious, as in *P. scariosa*.

Seeds

The seeds are geminate, elliptic to oblong and ovoid, and generally cymbiform in shape. Size, shape, and surface markings are diagnostically important. The seeds are unique in having the ventral surface excavated on one or both sides of a prominent ridge. However, the seeds of *P. bakeri* have the dorsal surface flat, with only a faint longitudinal groove down the center. On the ventral surface, the raphe is elevated above the normally excavated portions, thus giving the seed a triangular shape in cross section. In other taxa, the dorsal surface may be transversely ridged, as in *P. arizonica*, *P. palmeri*, and *P. popei*, and reticulate to scabrous in *P. congesta* and *P. rupestris*. *P. howelliana*, *P. serrata*, and *P. utahensis* have the dorsal surface smooth and shiny with faint alveolations, while the seeds of *P. pedicellata* are tuberulate. The remaining species are alveolate (pitted). The ridge is corrugated on one side in over half the taxa, while the remainder lack corrugations. The seed margins can be entire as in *P. alba*, *P. denticulata*, and others, or corrugated along part or all of the marginal edge. Corrugated margins are well represented in seeds of *P. bombycina*, *P. coerulea*, and *P. corrugata*.

Color variations occur, but brown predominates as in *P. neomexicana* and *P. pedicellata*. In such taxa as *P. constancei*, *P. pallida*, and *P. palmeri* the seeds are black, while in *P. bombycina*, *P. coerulea*, and *P. formosula*, they are dark brown. Reddish or reddish brown seeds are typical of *P. glandulosa*, *P. rafaelensis*, and *P. utahensis*.

The smallest seeds occur in *P. coulteri* (1.6 mm long), and the largest known are in *P. denticulata* (4 mm long). The light-colored, glutinous thickened band spoken of by Voss (1937) is a feature that develops during the ontogeny of the seeds. When immature, the seeds are either dark and turn light in color through a mottling pattern, or they are light and become dark when mature. The descriptions of seeds in this treatment are based on mature examples. They are considered the most important single feature in delineating taxa, and on the basis of the size, shape, and surface characters, several distinct groups can be arranged in an apparent phylogenetic order. These groupings are supported by other morphological features as well, namely leaf shape, pubescence, corolla shape and color, and duration of the plant. The branching pattern of the stem and inflorescence, the type of calyx segments, and the stamens and style, whether included or exserted, are also useful features.

Vesture

Considerable confusion exists as to the terminology used in describing the vesture of plants. The terms employed herein are defined in Appendix II to lend uniformity to their interpretation. The pubescence often consists of two or more types of intermixed hairs. There are two main types of trichomes, each exhibiting variation in size: (1) simple, unicellular trichomes, which vary in length and rigidity and may be erect, straight, or appressed; and (2) a stipitate-glandular type, which is usually multicellular. The stalk in the stipitate-glandular type varies in length and in number of cells. Sometimes the gland is sessile, or nearly so, and the stalk is often flattened.

Phylogeny

Constance (1963) indicates that the family appears to be a collection of morphological and geographical odds and ends, held together by floral and capsular features. He states, "I am not prepared to offer a complete system for *Phacelia*." However, Constance (1963) appears to have arrived at the most natural grouping of the genus *Phacelia* by recognizing three subgenera, Cosmanthus, Howellanthus, and Phacelia. The latter is the largest and most complex of the three and has been subdivided by Constance (l.c.) into the following species-groups: Crenulatae, Euglypta, Gymnobythus, Miltitzia, Pulchellae, Tanacetifoliae, and Whitlavia. The Crenulatae group, revised by Voss (1937), was the most complete study of the group prior to the present work. Gillett (1960b) indicates, "The current infrageneric classification of *Phacelia* is generally considered to be inadequate . . . and that considerably more evidence must be accumulated before the various species groups can be accorded classification that properly relates them to each other." The author agrees that natural generic and infrageneric relationships cannot be proposed until additional morphological, distributional, and cytological data have been accumulated. However, he is prepared to offer a tentative phyogenetic summary of relationships within the Crenulatae group. These data are subject to change as additional research may warrant.

Those species occurring from Mexico to South America present a problem in the formulation of a complete phylogenetic scheme. These southern taxa appear to be the most primitive and are certainly the least understood of all the Crenulatae group. Most are known only from the type collections. It would seem likely that the Crenulatae group has been derived

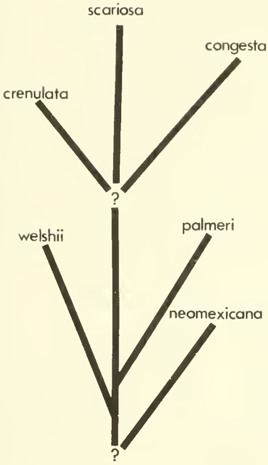


Fig. 1 A phylogenetic arrangement of the complexes in the Crenulatae group.

from some form of *Phacelia*, past or present, somewhere in Mexico or South America. The modern species suggest several avenues of migration from Mexico, which have contributed to the present diversity in morphology and distribution. Furthermore, the morphological, cytological, and distributional relationships of the subgeneric and sectional groups of *Phacelia* suggest either a polyphyletic origin or, if a monophyletic one, then a derivation possessing several major lines of development. Those main lines of development occurring within the Crenulatae group are outlined in Figures 1-7. The species are grouped together and arranged on the basis of similar morphological features and distribution. The following discussion is given to indicate which characters are considered to be advanced or primitive in this group.

Seeds provide the most important characters in differentiating entities. The most primitive species, which occur in Mexico, all have small seeds, which suggests that large seeds are probably a derived feature. This character seems to follow a south-to-north trend with the largest seeds occurring to the north. There have been several avenues of specialization with the primitive seeds having more surface markings and being thicker and narrower. The seeds of most taxa, except in *P. bakeri* and *P. argillacea*, uniformly have the ventral surface excavated on both sides of a prominent ridge. These latter entities have the raphe elevated above the usually excavated portions and would appear to have diverged from the more typical form. Seeds with a corrugated ridge appear to be primitive, and those with pitted (alveolate) and entire margins appear to be advanced. Light brown seeds are apparently primitive, and dark brown, black, and reddish types are apparently derived. Reticulate, transversely ridged, and smooth-surfaced seeds are also probably derived.

The corolla has developed along three basic lines. Primitive plants are those having blue to purple colored campanulate corollas and exserted stamens and styles. However, some of the less advanced species have small, pale, campanulate corollas with included stamens and styles. Thirdly, pale to white tubular corollas are present in the more advanced entities. These advanced forms have less attractive flowers and long exserted stamens and styles. The corolla lobes have developed along two major lines, with the *P. neomexicana* complex having denticulate or erose margins and the remainder having entire margins. The former feature is

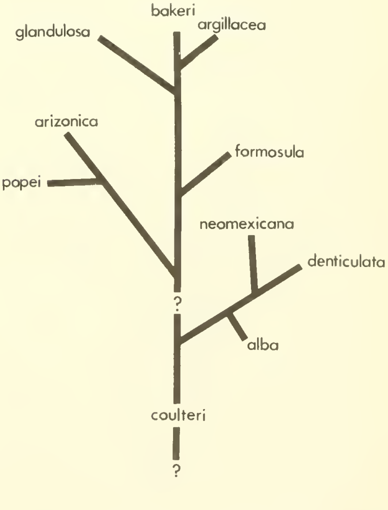


Fig. 2. A phylogenetic arrangement of the species in the *neomexicana* complex.

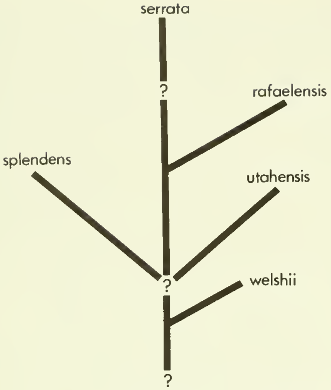

serrata
?
rafaelensis
splendens
utahensis
?
welshii
?

Fig. 3. A phylogenetic arrangement of the species in the *welshii* complex.

probably advanced, entire margins being primitive.

The scarious calyx segments of *P. scariosa* and *P. pedicellata* seem to be an advanced feature. This is supported by the fact that the calyx lobes are persistent in fruit and probably aid in dispersal. Small, narrow calyx segments are considered to be primitive.

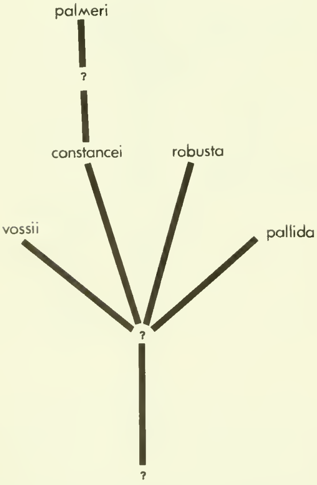

palmeri
?
constancei
robusta
vossii
pallida
?
?

Fig. 4. A phylogenetic arrangement of the species in the *palmeri* complex.

The spicate thyrsus type of inflorescence of the perennial, biennial, and some robust annual species is apparently advanced, while the variously branched systems developed in most annual and some biennial taxa appear to be primitive.

The primitive taxa do not follow the generalization that the perennial habit is more primitive than the biennial or annual type. The majority of entities are robust annuals, probably an inherited feature; biennial and perennial types appear to be derived. The primitive taxa

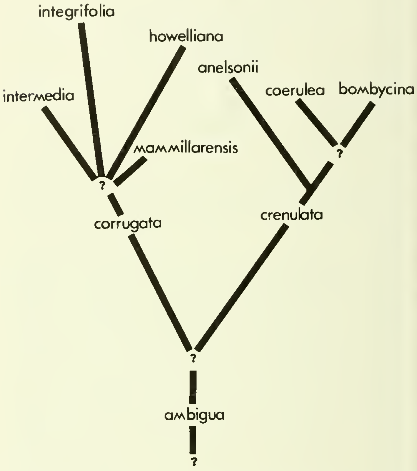

integrifolia
howelliana
anelsonii
intermedia
coerulea
bombycina
mammillarensis
?
?
corrugata
crenulata
?
ambigua
?

Fig. 5. A phylogenetic arrangement of the species in the *crenulata* complex.

possess an erect, usually branched, stout stem with a compound scorpioid inflorescence. Some advanced biennial and perennial entities have become specialized in the development of a spicate thyrsus inflorescence.

Entire or subentire leaves are apparently derived from compound leaves. The narrowly revolute type exhibited by *P. constancei* is considered to be a specialization, while the basal rosette common in the biennials and robust annuals appears to be a feature that has been retained during the phylogenetic development of leaves.

Members of the Crenulatae group are probably monophyletic and have developed along six major lines. These are

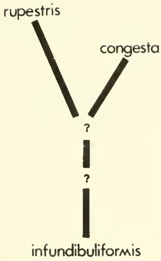


Fig. 6. A phylogenetic arrangement of the species in the *congesta* complex.

treated as complexes but are not accorded taxonomic status.

The hypothetical ancestor(s) of the Crenulatae group were apparently robust, densely glandular annuals with a branched stem, compound leaves and inflorescences, nonscarious sepals, and broadly campanulate blue or purple corollas. The seeds were light brown, small, excavated on both sides of the corrugated ridge, with thick entire margins, cymbiform, and elliptic to oblong in shape. Biennial and perennial types developed later in the phylogeny of the group. The primitive members of the *neomexicana* complex are apparently the most primitive and are considered to be closest to the ancestral forms. The *palmeri* complex arose somewhat later and extended more to the west of the *neomexicana* complex in its migration northward. The *congesta* complex had its origin somewhere in north central Mexico and possibly arose from the multiovulate *P. infundibuliformis* or some similar form. The *crenulatae* and *scariosa* complexes probably arose from taxa now extant in western Mexico. These six complexes are discussed and outlined in Figures 1-7.

Neomexicana complex

This complex is characterized by noncorrugated seeds, densely glandular pubescence, light brown seeds (except in *P. glandulosa*), compound leaves, and branched habit. *P. coulteri* is closest to the ancestral species. *P. alba*, *P. denticulata*, and *P. neomexicana* are related *to P. coulteri* but possess the advanced features of small, white to pale-colored corollas, and less robust habit. The migrational pattern of this complex has been northward out of Mexico through New Mexico to Wyoming and Montana. *P. popei* and *P. arizonica* have developed from a common ancestor, as indicated by their similarity in seed, pubescence, and vegetative features. The same is true of *P. formosula*, *P. glandulosa*, *P. bakeri*, and *P. argillacea;* however, the latter two have become specialized in the development of noncorrugated seeds. This is the only specialization away from the typically excavated seed type present in the rest of the Crenulatae group.

Welshii complex

This complex is characterized by the large reddish seeds, showy corollas, and generally long exserted stamens and style. All taxa are narrowly restricted endemics occurring in Utah, Arizona, and western Colorado. *P. welshii* is considered to be the most primitive on the basis of its smaller, somewhat brownish seeds and branched habit. *P. utahensis* and *P. splendens* probably had a common ancestor but have adapted to different edaphic situations and have therefore been isolated and selected out; judged on its robust branching habit and glandular pubescence, the former is probably more primitive. *P. rafaelensis* is related to *P. utahensis* and may have been derived from it. *P. serrata* is the most advanced species as characterized by its smaller, lighter-colored corollas, and shortly exserted stamens and styles.

Palmeri complex

P. vossii and *P. pallida* are the most primitive and, along with *P. robusta*, are restricted to the south central part of the U.S. and adjacent Mexico. The remaining two species, occurring in Utah, Arizona,

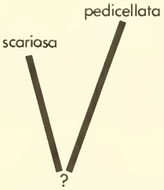


Fig. 7. A phylogenetic arrangement of the species in the *scariosa* complex.

and Nevada, are disjunct from the others. The species are distinguished by their pale tubular corollas, small black seeds, and perennial or biennial habit. *P. robusta* is related to *P. pallida* but is considered to be advanced on the basis of its larger, reddish seeds. *P. palmeri* possesses the advanced features of less-divided leaves and thin-margined seeds.

Crenulata complex

Although not lacking in a glandular pubescence, this complex displays more divergence from this primitive feature than does any other complex. There appears to be a bilateral development, with *P. crenulata* and its relatives becoming specialized with a mixed pubescence of long stipitate glands and short hairs and dark brown seeds. *P. anelsonii* and *P. coerulea* have small corollas with included stamens and style. The former is more advanced and possesses a thyrsoid inflorescence and more or less scarious sepals. The other line, of which *P. corrugata* is the primitive taxon, is characterized by light brown or dark brown seeds, short stipitate glands, and yellowish stems. *P. howelliana* and *P. integrifolia* are the most highly developed species in this line, the latter apparently being the most advanced on the basis of its lavender corollas and large, noncorrugated seeds. The former has large, dark brown seeds and bicolored corollas. The entire complex, with the exception of *P. intergrifolia*, possesses distinctly corrugated seeds.

Congesta complex

This complex is related to and has possibly been derived from *P. infundibuliformis* or some form close to it. *P. infundibuliformis* differs from other taxa in this complex only in its multiovulate, narrowly oblong capsule and overall vegetative appearance. The small white corollas, barely exserted stamens and style, and perennial habit of *P. rupestris* indicate that it is the most advanced species in this complex. The species of the *congesta* complex occur in the east central part of the range of the Crenulatae group.

Scariosa complex

This most advanced complex is characterized by distinctly scarious sepals, bicolored corollas, and large, corrugated, transversely ridged seeds. The species occurs in the southwesternmost part of the range of the group.

Distribution and Ecology

Members of the Crenulatae group occur mostly in western North America. The remaining species, *P. boliviana* Brand, *P. pinnatifida* Griseb. ex Wedd., and possibly others, occur in Peru, Bolivia, and Argentina. The center of distribution in North America, based on the greatest concentration of taxa, is Arizona and New Mexico.

In general, members of this group are desert plants that occur from near sea level to 5,000 feet elevation (up to 11,000 feet). Some are restricted to a particular geologic formation, such as *P. utahensis*, which grows only on the Arapian Shale formation. *P. bakeri* is restricted to montane or subalpine regions on talus or alpine slopes in Colorado, whereas *P. integrifolia* occurs mostly in deep sand. *P. splendens* is endemic to gypsiferous soil in western Colorado and northwestern New Mexico. The majority of taxa occur in the Lower Sonoran zone and are restricted to an isolated mountain range or valley. *P. corrugata*, *P. denticulata*, *P. glandulosa*, and others occur in the Upper Sonoran zone and generally have a wider distribution. *P. denticulata* is limited by the continental divide, occurring only on its eastern side. *P. congesta*, *P. pedicellata*, *P. arizonica*, *P. denticulata*, and *P. rupestris* are able to survive in the shade of overhanging ledges or as an understory of trees and shrubs.

An important isolating mechanism that helps to account for the wide distribution is the seasonal variation in phenology. The palmeri complex flowers in late summer and fall, whereas members of the welshii complex flower in spring and early summer. The foetid odor of some species is known to attract beetles, while bees and other insects are important pollinating agents in other species.

The light, cymbiform seeds are probably wind-dispersed. In addition to wind, birds are probably an important dispersing agent.

Cytology

Cave and Constance (1942, 1944, 1947, 1950, 1959) and Constance (1963) have made chromosome counts on about half the Crenulatae group, all of which are n=11. The uncounted members are mostly narrowly restricted endemic plants and include the following: *P. anelsonii*, *P. bakeri*, *P. boliviana*, *P. bombycina*, *P. constancei*, *P. coulteri*, *P. formosula*, *P. glandulosa*, *P. howelliana*, *P. integrifolia*. var. *texana*, *P. intermedia*, *P. pallida*, *P. serrata*, *P. utahensis*, *P. vossii*, and *P. welshii*.

Taxonomic Treatment

Phacelia Juss. Gen. 129. 1789.

Subgenus Phacelia Constance. Britt. 15:278. 1963.

Section Phacelia Brand. Das Pflanzenreich IV. 251:72. 1913

Group Crenulatae Constance. Britt. 15:279. 1963.

Annual, biennial, or perennial herbs from a taproot; stems simple to much branched, erect, ascending or prostrate, leafy, puberulent to hispid, strigose or variously glandular; leaves prevailingly alternate, entire to bipinnate, sometimes revolute, sessile to long petiolate; inflorescence of terminal, axillary, or thyrsoid, compound, scorpioid cymes; calyx divided nearly to the base, elliptic to linear, oblanceolate or spatulate, variously pubescent and sometimes accrescent; corolla white or lavender to blue, tubular, campanulate to rotate-campanulate, a pair of variously shaped scales attached to the base of each filament, these partially free from or completely attached to the tube, filament, or adjacent scale; stamens exserted or included within the tube, and inserted at the base of the corolla tube; style exserted or included within the tube, bifid 1/2-3/4 its length, capsule nearly bilocular by union of the placentae, ovoid to subglobose, variously pubescent and mostly glandular; mature seeds 4 (1, 2 or 4 in *P. amabilis* and *P. congesta*), light brown to black, favose, reticulate, entire to corrugated or tranversely ridged, excavated on both sides of a prominent ridge (except in *P. bakeri*) and mostly cymbiform.

Key to the species of the Crenulatae group

1a. Stamens and style included or nearly so 2
1b. Stamens and style exserted 2 mm or more 4

2a. Corolla tubular, light blue, lobes denticulate; plants of Colorado and Wyoming .... 15. *P. denticulata*
2b. Corolla campanulate or rotate-campanulate, lobes entire or at most crenulate 3

3a. Plants brittle, breaking easily; corolla 3-4 mm long, pale mauve to light blue; mature seeds dark brown .... 9. *P. coerulea*
3b. Plants not brittle; corolla ca. 6 mm long, lavender or white; seeds brown .... 4. *P. anelsonii*

4a. Pedicels shorter than the calyx; sepals not scarious in fruit 6
4b. Pedicels filiform (at least as long as the calyx lobes); sepals scarious in fruit; leaves pinnately compound, the divisions broad 5

5a. Sepals less than 3 times longer than broad; mature seeds 2.5 mm long or less; plants of lower Baja California and southwestern Sonora, Mexico .... 30. *P. scariosa*
5b. Sepals 3 or more times longer than broad; mature seeds 2.5 mm long or more; plants of central Baja California north to California, Arizona, and Nevada .... 25. *P. pedicellata*

6a. Corolla over 4 mm long, white or variously colored 13
6b. Corolla small (4 mm long or less), white, blue, or lavender 7

7a. Plants prostrate, diffusely branched (at the base); mature seeds 1.8-1.9 mm long, ovate, transversely ridged; corolla white .... 6. *P. arizonica*

7b. Plants erect, mature seeds mostly over 2 mm long, if smaller then not with the above combination of characters 8

8a. Corolla lobes entire; mature seeds with the ridge corrugated or the dorsal surface reticulate 11

8b. Corolla lobes erose or denticulate; mature seeds pitted, margins and ridge entire 9

9a. Corolla white or pale colored, 3-4 mm long .... 1. *P. alba*

9b. Corolla blue or purple, 4-5 mm long 10

10a. Stems thick, robust; corolla 4-5 mm long, bluish purple; mature seeds 1.6-1.9 mm long; plants endemic to the states of Hidalgo and Zacatecas, Mexico .... 13. *P. coulteri*

10b. Stems weak; corolla 4 mm long, blue; mature seeds 3.2-3.3 mm long; plants of Arizona and New Mexico .... 22. *P. neomexicana*

11a. Corolla white; mature seeds 2.1-2.7 mm long, the ridge not corrugated, dorsal surface reticulate; plants from southeastern Arizona eastward .... 29. *P. rupestris*

11b. Corolla blue to light violet; seeds 2.5-3.2 mm long, the ridge corrugated 12

12a. Corolla bicolored (tube white, lobes blue to lavender), campanulate; seeds ovate, ridge corrugated, margins entire; plants from western Arizona westward .... 3b. *P. ambigua* var. *minutiflora*

12b. Corolla not bicolored, light blue to lavender, rotate; seeds elliptic to oblong, ridge and margins corrugated; endemic to Coconino County, Arizona .... 31. *P. serrata*

13a. Corolla distinctly tubular, white or pale colored 14

13b. Corolla campanulate, purple, blue, lavender, or white (appearing tubular in some pressed specimens) 19

14a. Plants annual or biennial (possibly perennial in *P. pallida*); north of Nuevo León, Mexico 15

14b. Plants perennial; endemic to the state of Nuevo León, Mexico .... 34. *P. vossii*

15a. Seeds brown or reddish brown, 2.9 mm long or more 16

15b. Seeds black, 2.9 mm long or less 17

16a. Seeds 3.5-4 mm long; cauline leaves sessile (or nearly so), auriculate; plants of Utah .... 27. *P. rafaelensis*

16b. Seeds 2.9-3.7 mm long; cauline leaves distinctly petiolate, not auriculate; plants of Kansas, Oklahoma, Texas, and Mexico .... 28. *P. robusta*

17a. Inflorescence thyrsoid; stems solitary or if branched then near the base .... 24. *P. palmeri*

17b. Inflorescence open; stems branched throughout, especially at base 18

18a. Leaves revolute, narrowly linear or lanceolate (less than 1.5 cm wide); plants of Utah and Arizona .... 11. *P. constancei*

18b. Leaves not revolute, broadly oblong or lanceolate (mostly over 1.5 cm wide); plants of Texas and adjacent Mexico .... 23. *P. pallida*

19a. Leaves pinnately or bipinnately compound, finely dissected 20

19b. Leaves simple or if compound not finely so, the divisions broad (over 5 mm wide) 25

20a. Corolla violet; plants endemic to Jackson County, Colorado .... 16. *P. formosula*
20b. Plants not as above 21

21a. Pubescence of the leaves mostly unicellular, puberulent to hispid; plants native from western and southern New Mexico, southward and eastward (except in *P. argillacea* which is endemic to Utah) 22
21b. Leaves mostly with multicellular, stipitate-glandular hairs; native from central New Mexico northward and westward 24

22a. Flowers violet to light blue; seeds more or less excavated on one side of the ventral ridge; plants endemic to the Green River Shale formation in Utah County, Utah .... 5. *P. argillacea*
22b. Flowers blue to purple; seeds excavated on both sides of the ventral ridge 23

23a. Seeds 1.8 mm long, ovate; ultimate leaf divisions mostly less than 4 mm wide .... 26. *P. popei*
23b. Seeds over 1.8 mm long, elliptic to oblong; ultimate leaf divisions mostly over 5 mm wide .... 10. *P. congesta*

24a. Seeds not excavated ventrally; plants east of the Continental Divide in Colorado and New Mexico .... 7. *P. bakeri*
24b. Seeds excavated ventrally; plants west of the Continental Divide in Wyoming, Montana, and Idaho .... 17. *P. glandulosa*

25a. Corolla not distinctly bicolored, blue, purple, or white 28
25b. Corolla distinctly bicolored, the tube white or yellow, the lobes blue 26

26a. Cauline leaves sessile, auriculate, plants robust, 0.8-5.8 dm tall, endemic to Sanpete and Sevier counties, Utah .... 33. *P. utahensis*
26b. Cauline leaves distinctly petiolate; plants not especially robust, less than 2.7 dm tall, more eastern in distribution 27

27a. Stems branched at base; leaves simple, strigose and glandular; corolla tube white; seeds corrugated on the margins and ridge, dorsal surface smooth .... 18. *P. howelliana*
27b. Stems simple or branched above; leaves essentially glabrous, some of the lower usually compound; corolla tube yellowish; seeds essentially lacking corrugations, dorsal surface deeply pitted .... 32. *P. splendens*

28a. Corolla white; plants endemic to Saline Valley, Inyo County, California .... 2. *P. amabilis*
28b. Corolla pale blue, purple, or lavender (rarely white); plants widespread or if endemic not as above 29

29a. Corolla lavender; seeds lacking ventral corrugations .... 19a. *P. integrifolia* var. *integrifolia*
29b. Corolla pale blue to purple; seeds corrugated ventrally 30

30a. Stamens and style exserted 4 mm or less; mature seeds 2.9 mm long or less 31
30b. Stamens and style exserted over 4 mm; mature seeds over 2.0 mm long 32

31a. Mature seeds 2.2-2.5 mm long; dark brown; plants very brittle annuals .... 8. *P. bombycina*
31b. Mature seeds 2.7-2.9 mm long; brown; plants not especially brittle .... 20. *P. intermedia*

32a. Mature seeds corrugated only on the ridge; pubescence of the stems densely hispid, glandular above .... 3a. *P. ambigua* var. *ambigua*

32b. Seeds with the margins and ridge corrugated; pubescence of the stems mostly glandular, sometimes finely so 33

33a. Glandular pubescence of the stems and herbage mostly multicellular 34

33b. Glandular pubsecence of the stems and herbage stipitate but not multicellular 35

34a. Corolla lavender to purple, 4.5-6 mm long; anthers blue green; stems often reddish; mature seeds reddish brown, 2.4-3 mm long; plants of southeastern New Mexico and adjacent Texas .... 19b. *integrifolia* Torr. var. *texana*

34b. Corolla blue, 6 mm long or longer; anthers always yellow; stems green or yellow green; mature seeds light brown, 3.1-4 mm long; plants of northwestern New Mexico, Arizona, Colorado, and Utah .... 12. *P. corrugata*

35a. Leaves narrowly oblong, mostly less than 1 cm wide, glandular pubescence of the leaves and lower part of the stems short stipitate, the nonglandular hairs mostly fine, retrorse .. 14a. *P. crenulata* var. *angustifolia*

35b. Leaves mostly well over 1 cm wide, glandular pubescence of the leaves and stems stipitate-multicellular, nonglandular hairs spreading 36

36a. Stems usually reddish at least below; mature seeds with a dark center dorsally and lighter margins; plants of western Utah and Arizona westward to California and Nevada .... 14b. *P. crenulata* Torr. var. *crenulata*

36b. Stems green; mature seeds uniform in color dorsally; plants endemic to Coconino County, Arizona 37

37a. Corolla lavender to white, campanulate, 5-6 mm long; leaves undulate to regularly dentate, oblong to lanceolate; seeds uniformly brown; plants endemic to Kane and Garfield counties, Utah .... 21. *P. mammillarensis*

37b. Corolla dark blue, tubular to funnelform, 5-8 mm long; leaves irregularly crenate to dentate, lanceolate; seeds brown ventrally and reddish dorsally; plants endemic to Coconino County, Arizona .... 35. *P. welshii*

1. *Phacelia alba* Rydberg

Fig. 8

Phacelia alba Rydb., Bull. Torr. Bot. Club 28:30. 1901.

Holotype: Colorado: Costilla Co.: Sangre de Christo Creek, 2 July 1900. Rydberg and Vreeland. 5755. (NY?); Isotype (RM!).

Paratypes: Colorado: Clear Creek County: Valley of Upper Arkansas River, 1873. J. Wolfe, 99. (NY): head waters of Clear Creek, 1861, C. Parry. 314 (GH, NY); New Mexico: Lincoln Co.: Ruidoso Creek. White Mountains, 1 July 1895, E. Wooton. s.n.. (NY).

Phacelia neomexicana Thurber ex Torr. var. *alba* (Rydb.) Brand. Das Pflanzenreich IV. 251:83. 1913.

Phacelia neomexicana Thurber ex Torr. var. *coulteri* subvar. *folisissima* Brand. Das Pflanzenreich IV. 251:84. 1913. Holotype: Mexico: state of Chihuahua: near Colonia Garcia. 13 July 1899, Townsend and Barber, 129, (NY); Isotypes (CAS, MEXU, POM, RM. UC, UC, US).

Phacelia glandulosa Nutt. ssp. *eu-glandulosa* Brand var. *elatior* Brand, Das Pflanzenreich IV, 251:82-83. 1913. in part. Holotype: Wyoming: Albany Co.: Jelm. 12 August 1900, A. Nelson, 8053. (GH, POM, RM).

Plants annual, 0.5-7 dm tall; stems simple to much branched. erect or ascending. leafy. puberulent. setose to hirsute and stipitate-glandular. especially in the inflorescence; leaves irregularly lobed to bipinnate, 2-10 cm wide. strigose to setose, slightly to moderately stipitate-glandular, long petiolate below to sessile or subsessile above; inflorescence of dense terminal compound scorpioid cymes. densely glandular and puberulent to hirsute, the cymes 1-2 cm long in flower to 8 cm long in fruit, pedicels 0.8-1 mm long; sepals linear to oblanceolate, 3.5-4 mm long, 0.5-1 mm wide, finely glandular and somewhat setose; corolla campanulate, white (sometimes pale purple), 3-4 mm long and broad, lobes pubescent and denticulate; capsule ovoid to subglobose, 3-3.3 mm long, 2.5-2.9 mm wide, puberulent and quite glandular (the partition oblanceolate); mature seeds elliptic to oblong, light to dark brown, 2.4-3 mm long, 1.4-1.5 mm wide, uniformly alveolate throughout and cymbiform, the ventral surface shallowly excavated on both sides of the ridge and lacking corrugations, the margins thick and entire (Fig. 9). Collections: 207 (5); representative: C. Parry 314, 1861 (GH, NY); D. Atwood 1975, 1962, 1963a (BRY, NY, US); M. Jones 511 (POM).

Habitat.— Dry clay-loam or sandy draws and flats, fields, meadows, and gravelly hillsides. From 6,000 to 9,500 feet. Growing on the short grass prairie, sagebrush belt, and pinyon-juniper communities at the lower elevations and associated with aspen, spruce, fir, or pine forests at the higher elevations. Late May to early October.

Distribution.— Laramie and Albany cos., Wyoming, southward through central Colorado, New Mexico, and adjacent Chihuahua, Mexico, westward to Graham and Apache cos., Arizona, and Sevier, Wayne, Garfield, and Washington cos., Utah (Map 1).

The material cited by Brand (1913) for *P. glandulosa* ssp. *eu-glandulosa* var.

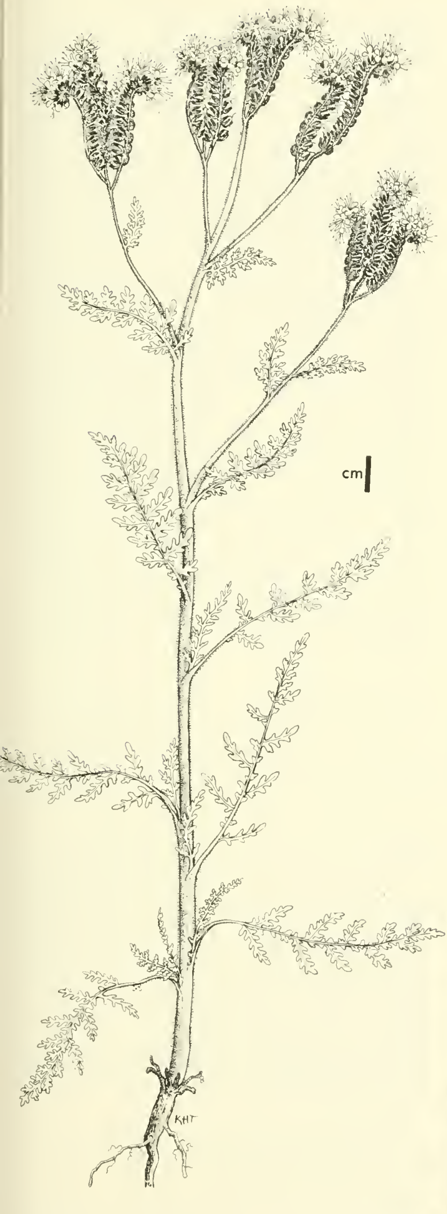


Fig. 8. *Phacelia alba* Rydberg. L. Higgins 2229 (BRY).

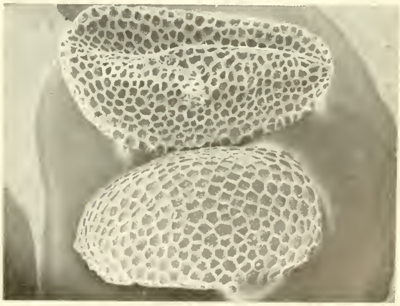


Fig. 9. Dorsal and ventral view of the seeds of *P. alba* Rydberg. D. Atwood 1975 (BRY).

elatior Brand (Nelson 8053) belongs to *P. alba*.

2. *Phacelia amabilis* Constance

Phacelia amabilis Constance. Madroño 7:56-59. 1943.

Holotype: California: Inyo County: Saline Valley, 21 April 1942, A. Alexander and L. Kellogg 2681 (UC!); Isotype (UC).

Plants annual; stems stout, branched above, stipitate-glandular, puberulent, and hispid; leaves petiolate, oblong to oblong-ovate, 8-15 cm long, 3-5 cm wide, pinnatifid, upper leaves reduced and less deeply divided; inflorescence of compound scorpioid cymes, the cymes 5-12 cm long, pedicels 2-3 mm long; sepals lanceolate, 3-5 mm long, 1-2 mm wide; corolla broadly campanulate, white, 7-8 mm long, 8-12 mm wide; stamens and style exserted 5 mm or more; capsule ovoid, 3-4 mm long, 2-3 mm wide; immature seeds apparently 2 or 4, 3-4 mm long, thin and pale, ventral surface excavated on each side of the prominent ridge; collections: 1 (0); representative: A. Alexander and L. Kellogg 2681 (UC).

Distribution and Habitat.— Apparently endemic to Saline Valley, Inyo County, California, along Hunter Creek at an elevation of 1,800 feet.

3. *Phacelia ambigua* Jones

Plants annual, 0.2-5.7 dm tall; stems simple to much branched, hispid, puberulent, and stipitate-glandular; leaves simple to pinnately compound, petiolate to sessile above, the margins various, strigose to hispid and stipitate-glandular, 0.5-13 cm long, 0.5-4.5 cm wide; inflorescence of compound scorpioid cymes, the cymes elongating to 12 cm in fruit, pubescence as for the stem; sepals elliptic to oblanceolate, 2.7-5.1 mm long, 1-1.3 mm wide, puberulent, hispid, and stipitate-glandular; corolla campanulate to rotate-campanulate, purple or dull lavender, 4-10 mm long and broad, pubescent; stamens and style exserted 2-10 mm; style bifid, pubescent below; capsule globose to subglobose, 3-3.5 mm long, 2.5-3.4 mm wide, puberulent and glandular; mature seeds 4, ovate, reddish to brown, 2.5-3.3 mm long, 1.3-1.8 mm wide, alveolate, cymbiform, the ventral surface excavated on both sides of the ridge, the ridge corrugated on one side.

Key to the varieties of *P. ambigua*

1. Corolla 4 mm long or less; style 6.5 mm long or less; calyx in fruit less than 4 mm long .... var. *minutiflora*
1. Corollas over 4 mm long; style 9 mm long or more; calyx in fruit 4 mm long .... var. *ambigua*

3a. var. *ambigua*

Phacelia ambigua Jones, Contr. West. Bot. 12:52. 1908.

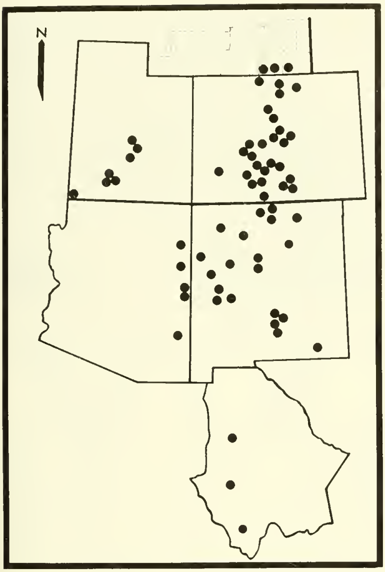
Holotype: California: San Bernardino Co.: Needles, 5 May 1884, M. Jones 3822. (POM!); duplicates (NY, RM, UC, US). Paratypes: Arizona: Coconino Co.: Hole in the Rock, 13 April 1894, M. Jones s.n., (?); Nevada: Lincoln Co.: Caliente, 29 April 1904, M. Jones, s.n., (?).

Phacelia crenulata Torr. in Wats. var. *ambigua* (Jones) Macbride. Contr. Gray Herb. 49:25. 1917.

Plants annual, 0.5-5.7 dm tall; stems simple to much branched, usually more leafy toward base; leaves 0.5-13 cm long, 0.5-4.5 cm wide, strigose to hispid, usually only with scattered glands, reduced from the base upward; cymes elongating to 12 cm in fruit; sepals 3.2-5.1 mm long, 1-1.3 mm wide; corolla campanulate, purple to blue, 5-10 mm long and wide, pubescent; stamens and style exserted 9 mm or more; style bifid 2/3 its length, puberulent and glandular below; capsule 3.3-3.5 mm long, 3-3.4 mm wide, puberulent and stipitate-glandular; mature seeds 3.3 mm long, 1.5 mm wide. Collections: 250 (30); representative: E. Palmer 625 (NY); M. Jones 5018 (NY, POM, RM, UC, US); C. Pringle s.n. (CAS, GH, NY); J. Howell 3504 (RSA); D. Atwood 2210, 2220a, 2294, 2296, 2303, 2310, 2319, 2353 (BRY).

Habitat.— Growing on a wide variety of soils in the lower Sonoran Desert from 490 to 5,000 feet elevation. February to mid-June.

Distribution.— Southern Nevada and southwestern Utah in Washington Co.,



Map 1. Southern Wyoming, Utah, Colorado, Arizona, New Mexico, and Chihuahua, Mexico. Distribution of *P. alba* Rydberg.

southward through Arizona (except for Navajo and Apache cos.,) and southeastern California (Map 2).

Phacelia ambigua has been treated as a variety of *P. crenulata*, which it closely resembles. However, the former species appears to be more uniform throughout its range than does the latter. Also, to treat *P. ambigua* at infraspecific rank would require the inclusion of other closely related taxa, namely *P. bombycina* W. & S. and *P. amabilis* Constance. In order to understand the complete relationships between these taxa additional field and greenhouse studies are needed. These studies may demand nomenclature changes, but until such studies are carried out the present treatment provides a more uniform arrangement of the entities involved.

3b. var. *minutiflora* (Voss in Munz) Atwood comb. nov.

Fig. 10

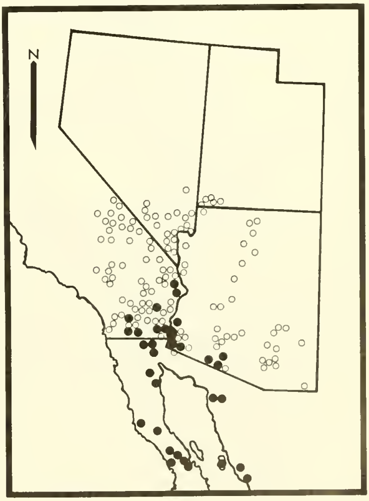
Phacelia minutiflora Voss in Munz, Man So. Calif. Bot. 409, 600. 1935.

Holotype: California: Imperial Co.: 2 miles north of Cargo Muchacho Mountains, 5 April 1932, P. Munz and L. Hitchcock 12141 (POM!).

Phacelia crenulata Torr. in Wats. var. *minutiflora* (Voss) Jeps., Fl. Calif. 3:266. 1943.

Plants annual, 0.2-4.5 dm tall; stems simple or variously branched, hispid, puberulent and stipitate-glandular (especially in the inflorescence); leaves 0.5-11 cm long, 0.5-3.5 cm wide, strigose to hispid and often quite glandular, the lower with longer petioles than the upper reduced leaves, cymes elongating to 7 cm in fruit; sepals 2.7-3.8 mm long, 1 mm wide, corolla rotate-campanulate, tube white, lobes lavender to blue, pubescent, 4 mm long and broad; stamens and style exserted 2 mm or less; style bifid 2/3 its length, puberulent and glandular below; capsule 3-3.2 mm long, 2.5-3 mm wide, puberulent and glandular; mature seeds 2.5-3.2 mm long, 1.3-1.8 mm wide (Fig. 11). Collections: 89 (4); representative: E. Palmer 626 (NY); T. Kearney and R. Peebles 10941, 10963, 11016 (US); D. Atwood 2320, 2355, 2352, 2341 (BRY); I. Wiggins 9669 (RSA, UC).

HABITAT.— Sandy to rocky desert flats, washes and slopes from near sea level to 2,200 feet. Common in *Larrea*, *Ambrosia*, *Atriplex*, *Fouguieria*, and *Cercidium* communities. Late December to late April.



Map 2. Utah, Nevada, Arizona, California, and adjacent Mexico. Distribution of *P. ambigua* Jones: ○ var. *ambigua;* var. *minutiflora.* ●

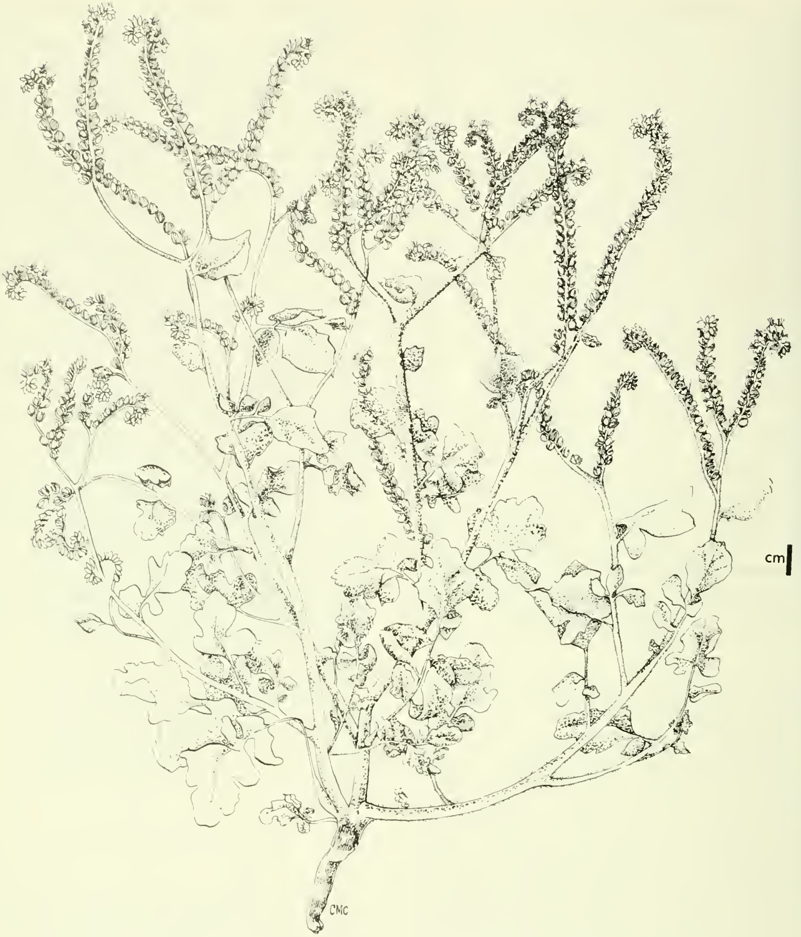


Fig. 10. *Phacelia ambigua* Jones var. *minutiflora* (Voss in Munz) Atwood. D. Atwood 2341 (BRY).

Distribution.— Southwestern Arizona in Maricopa, Pima, and Yuma cos., and westward to San Bernardino Co., California, south into Baja California and Sonora, Mexico (Map 2).

4. *Phacelia anelsonii* Macbride
Fig. 12

Phacelia anelsonii Macbride, Contr. Gray Herb. 49:26. 1917.

Holotype: Nevada: Lincoln Co.: Meadow Valley Wash, 28 April 1902, L. Goodding 635 (RM!).

Erect annual, 1-5.5 dm high; stems terete, usually simple covered with brownish stipitate glands, leafy throughout; leaves narrowly to broadly oblong, pinnately cleft, 1.5-8 cm wide, pubescence brownish, stipitate-glandular, with a few non-glandular hairs, pedicels from 3 cm long on the lower part of the stem to nearly sessile on the upper part, the pin-

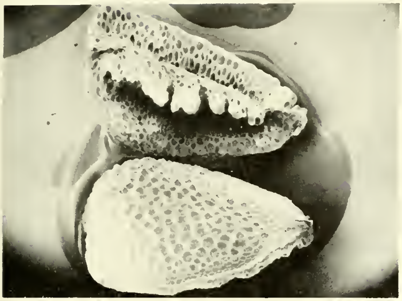


Fig. 11. Dorsal and ventral view of the seeds of *P. ambigua* Jones var. *minutiflora* (Voss in Munz) Atwood. D. Atwood 2320 (BRY).

nae somewhat reduced toward the base of leaf, margins crenate; inflorescence racemose to paniculate, usually terminal on the upper half of the stem, sometimes on leafy lateral branches, individual cymes 1-5 cm long, setose and glandular pubescent; corolla light violet or white, rotate-campanulate, 6 mm long and wide; sepals oblanceolate to spatulate, 3-6 mm long, 1-2 mm wide, setose to glandular, 1-2 mm longer than the capsule; stamens included, anthers yellow; style included, 3.5-4.8 mm long, shorter than the stamens, cleft 2/3 its length, glandular and puberulent at the base; capsule oval, 3.3-3.7 mm long, glandular spotted throughout and pilose on the upper half; mature seeds 4, oblong, 2.7-3.4 mm long, 1-1.3 mm wide, light brown, margins entire, ventral surface strongly alveolate, divided by a prominent ridge, ridge corrugated along one side, dorsal surface alveolate (Fig. 13). Collections: 30 (1); representative: L. Goodding 635 (RM); R. Barneby 2937 (CAS, RSA): S. Welsh, D. Atwoood, and E. Mathews 9542 (BRY); L. Higgins 499 (BRY).

HABITAT.— Commonly in shady places at the base of sandstone and limestone cliffs or among rocks and in sandy to gravelly washes, 2,000 to 5,000 feet elevation. Usually locally scattered, April to May.

DISTRIBUTION.— Lincoln Co., Nevada, southward to Washington Co., Utah, Inyo and San Bernardino cos., California (Map 3).

Macbride (1917) in his original description of *P. anelsonii* says, "this is the plant which Goodding, when he described his *P. foetida* . . . took to represent *P. palmeri* Wats., a very different plant with exserted stamens and corrugated

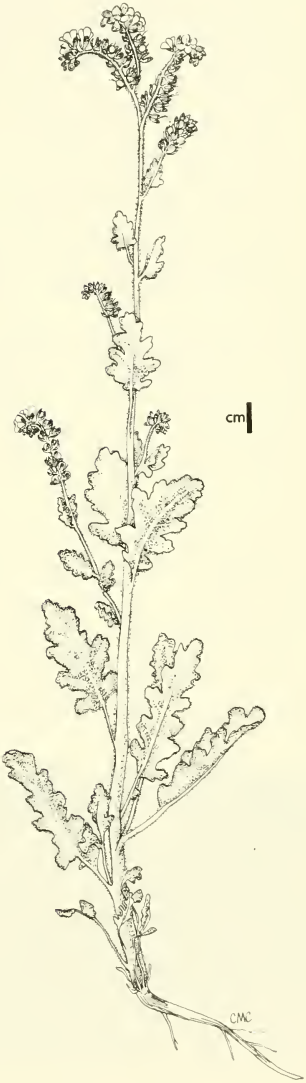


Fig. 12. *Phacelia anelsonii* Macbride. H. Ripley and R. Barneby 3496 (CAS).

seeds." It is not known from whence Macbride drew this conclusion, but it supports the observations of the author that *P. foetida* is the same entity as *P. palmeri*.

P. anelsonii is related to *P. crenulata* and *P. amabilis* as indicated by both leaves and seed characters. *P. anelsonii* is easily distinguished from them by the included stamens and style, a feature which it has in common with *P. coerulea* and *P. denticulata*. Detailed observations of the type specimens, as well as other collections, revealed the presence of corrugations along one side of the ridge in some seeds of *P. anelsonii*. Both *P. crenulata* and *P. amabilis* have the corrugated ridge. Macbride (1917) and Voss (1937) have indicated that the seeds lack corrugations.

John Thomas Howell was the first to report this taxon for Washington Co., Utah, and San Bernardino Co., California (1941), and for Inyo Co., California (1942). Two collections from Washington Co., Utah (R. Barneby 2937 and B. Wood 140), are more robust in habit and have unusually large parts.

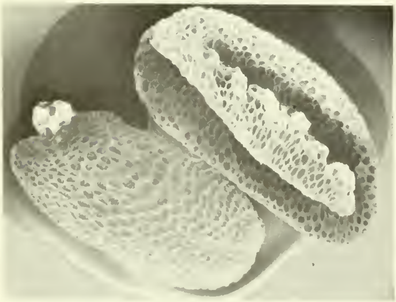
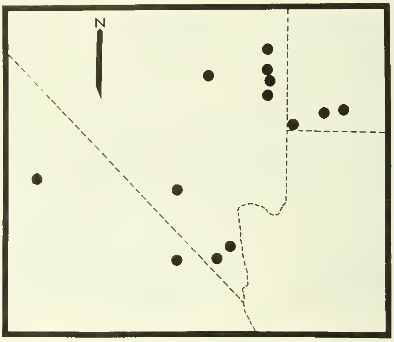


Fig. 13. Dorsal and ventral view of the seeds of *P. anelsonii* Macbride. R. Barneby 2937 (CAS).



Map 3. Southwestern Utah, southern Nevada, and California. Distribution of *P. anelsonii* Macbride.

5. *Phacelia argillacea* Atwood

Phacelia argillacea Atwood. Phytologia 26(6):437. 1973.

Phacelia glandulosa Nutt. var. *argillacea* Atwood in Welsh & Moore, nomen. nudum. Holotype: Utah Co.: Spanish Fork Canyon, Clear Creek ca. 6 mi west of Soldier Summit, 18 August 1971, D. Atwood et al. 3091 (BRY); Isotypes, to be distributed; Pleasant Valley Junction (Colton), Wasatch Mountains, August 1883, M. E. Jones s.n. (US!); Isotypes (CAS, CAS, NY, NY, POM, UC, UC). Paratypes: Utah: Utah Co.: Clear Creek near Soldier Summit, 6 July 1894, M. E. Jones 5591 (NY, POM, UC).

Plants annual, 1-3.6 dm tall; stems finely pubescent; leaves oblong in outline, pinnatifid, 0.8-5 cm long, 0.5-1.5 cm wide, strigose, petiolate; inflorescence of compound scorpioid cymes, stipitate-glandular and setose to hirsute, pedicels 0.7-1 mm long, cymes elongating to 7.5 cm in fruit; sepals elliptical to oblanceolate, 2-3.8 mm long, 1 mm wide, stipitate-glandular and hirsute to setose; corolla campanulate, bluish violet, ca. 5 mm long and broad, lobes pubescent; stamens and style exserted ca. 7 mm; capsule subglobose, 3.2-3.3 mm long, 2.3-2.4 mm wide, glandular and setose; mature seeds 4, brown, ovate to elliptic, 2.4 mm long, 1.1 mm wide, pitted, the ridge curved and more or less excavated on one side. Collections: 3 (1); representative: M. Jones s.n. (CAS, NY, POM, RM, UC, US); M. Jones 5591 (NY, POM, UC); D. Atwood 3091 (BRY).

HABITAT.— The species apparently grows on gravelly hillsides of the Greenriver formation between 6,500 and 7,000 feet, July to August.

DISTRIBUTION.— Known only from Utah Co., Utah.

This species is related to both *P. glandulosa* and to *P. bakeri* but can be distinguished by its more nearly glabrous herbage, smaller capsule, flowers, and different seeds.

6. *Phacelia arizonica* A. Gray
Fig. 14

Phacelia arizonica A. Gray, Syn. Fl. II, 1:394. 1878.

Lectotype: Arizona: Maricopa Co.: plains of the upper Gila, 15 April 1880, E. Greene s.n. (GH!); duplicate (CAS).

Phacelia popei Torr. & Gray var. *arizonica* (Gray) Voss, Bull. Torr. Bot. Club 64:94-95. 1937.

Low diffusely branched (at the base), prostrate annual, 0.2-2.1 dm tall (up to 4 dm in extreme forms); stems slender, 1-many, hispid to villous and glandular, often reddish; leaves larger and denser at the base, oblong to linear in outline, sessile above to short petiolate below deeply lobed to pinnatifid, 1-5 cm long, 0.5-2 cm wide, densely strigose, inflorescence terminal, cymes densely flowered, the flowers subsessile (pedicels to 0.5 mm long), densely covered with small glandular and short simple hairs, with some longer simple hairs intermixed; sepals oblong to elliptic, 2.5-4 mm long, 1 mm wide, hirsute; corolla campanulate, white or rose white, (often reddish in bud), 3-4 mm long and broad, lobes pubescent and shallowly erose; stamens and style exserted 3-4.5 mm; style bifid 3/4 its length, the lower 1/2 puberulent and sometimes finely glandular; mature seeds 4, ovate and more or less cymbiform, brown, 1.8-1.9 mm long, 1.2-1.3 mm wide, alveolate, ventral surface excavated on both sides of the ridge, dorsal surface alveolate and transversely ridged (Fig. 15). Collections: 104 (2); representative: C. Pringle s.n. (NY); L. Goodding 1035 (NY, UC, US); M. Jones 28501, 28503 (POM); D. Atwood 2200a (BRY, CAS, NY, WTS, B); L. Higgins 2814 (BRY); D. Atwood 2186 (B, BRY, CAS, NY, WTS).

HABITAT.— Common along roadsides, sandy flats, and gravelly hillsides, from 1,600 to 2,500 feet. Often growing with *Prosopis*, *Quercus*, *Juniperus*, or grass communities, mid-February to late June.

DISTRIBUTION.— Arizona from Maricopa Co. southward into Sonora, Mexico, and eastward to Sierra and Luna cos., New Mexico (Map 4).

This species was treated as a variety of *P. popei* T. and G. by Voss (1937), but is easily distinguished as a species on the basis of its smaller, white, glandless corolla, prostrate habit, less-dissected leaves and nearly leafless stems. However, the two are similar in seed characters and in the much-branched habit. *P. popei* has erect to ascending and more rigid stems in contrast to the slender, prostrate stems of *Phacelia arizonica*. Gray (1878) did not designate a type specimen. Therefore, the author has chosen the collection of Greene, "on the plains of the upper Gila," as the lectotype.

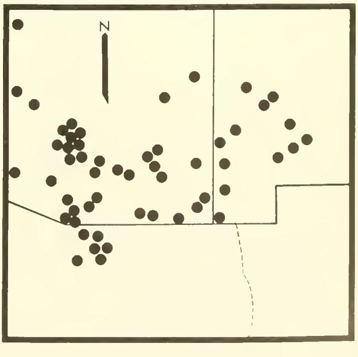
7. *Phacelia bakeri* (Brand) Macbride
Fig. 16

Phacelia bakeri (Brand) Macbride. Contr. Gray Herb. n. ser. 49:24. 1917.

Phacelia crenulata Torr. ex S. Wats. var. *bakeri* Brand, Das Pflanzenreich IV. 251:78. 1913. Holotype: Colorado: Ouray Co.: Ouray, 10 August 1901, C. F. Baker 758 (GH!); duplicates (NY, POM, RM, UC, US).

Phacelia glandulosa Nutt. subsp. *eu-glandulosa* Brand var. *australis* Brand, Das Pflanzenreich IV. 251:82-83. 1913, in part. Lectotype: Colorado: Conejos Co.: Cumbers, 7 September 1899, C. F. Baker 549 (US!); duplicates (GH, NY, POM, RM, RM). Paratypes: Colorado: El Paso Co.: Manitou, 15 July 1903, C. Clements 47.1 (RM), in part; Hinsdale Co.: Lake Fork River, Lake City, July 1893, C. A. Purpus 618 (UC, UC).

Annual, 0.5-4.8 dm tall; stems simple or branched, with multicellular stipitate glands, pilose to somewhat hirsute; leaves pinnately divided, the pinnae irregularly crenate to dentate, 2-8 cm long, 0.5-3 cm wide, reduced upwards, petioles 0.5-4 cm long, dorsal surface strigose, ventral surface strigose, glandular and setose along



Map 4. Southern Arizona and adjacent Sonora, Mexico, and western New Mexico. Distribution of *P. arizonica* Gray.

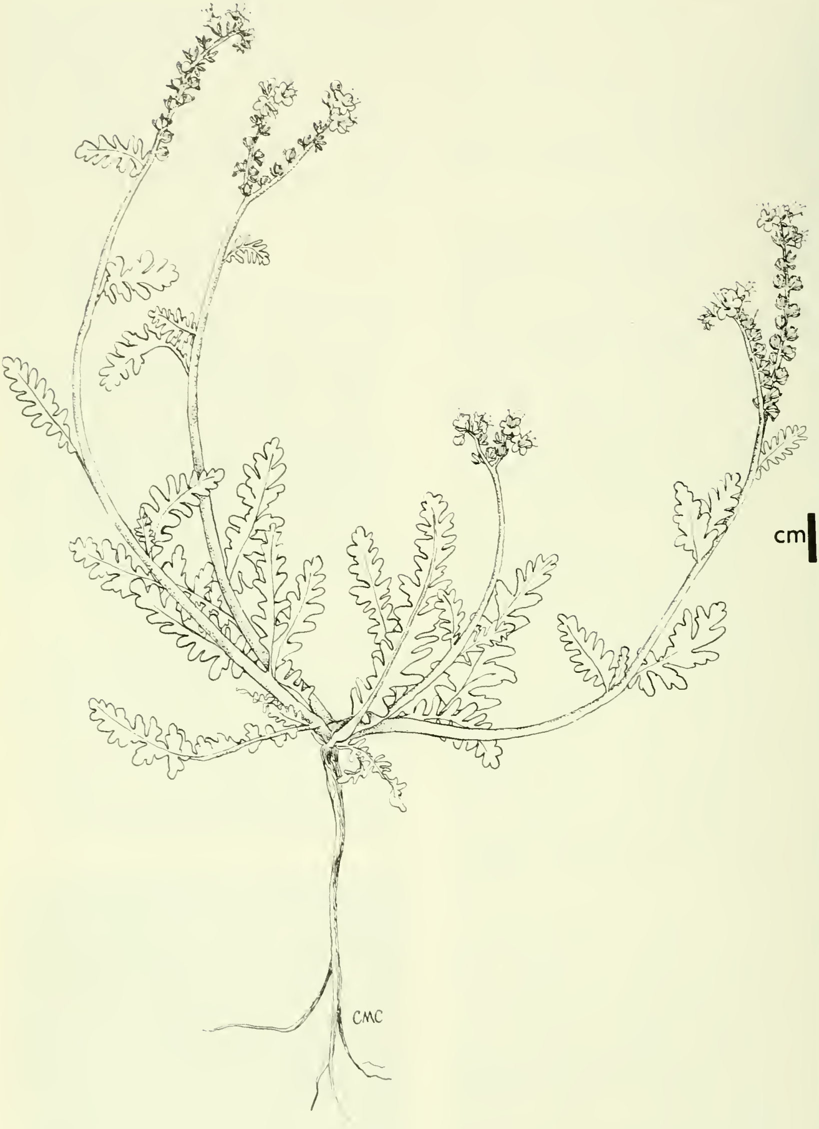


Fig. 14. *Phacelia arizonica* Gray. L. Higgins 2814 (BRY).

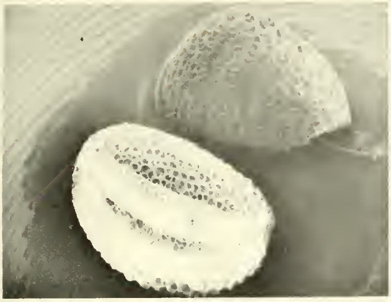


Fig. 15. Dorsal and ventral view of the seeds of *P. arizonica* Gray. D. Atwood 2186 (BRY).

the veins; inflorescence of compound scorpioid cymes, terminal on the main stem and lateral branches, setose to puberulent and glandular, pedicels 1-2 mm long; sepals oblanceolate to narrowly spatulate, 1-1.5 mm longer than the capsule, setose to puberulent and glandular; corolla campanulate, violet to dark blue, 7-8 mm long, 5-7 mm wide, pubescent; stamens exserted 5-9 mm, anthers greenish, filaments bluish; style exserted bifid 2/3 its length and pubescent on the lower 1/3; capsule oblong to oval, 2.5-4 mm long, 3-3.2 mm wide, setose and glandular; mature seeds elliptic, brown, 2.7-3 mm long, 1.3-1.6 mm wide, ventral surface pitted with a central ridge gradually tapering toward the margins, excavations lacking on each side of ridge, dorsal surface flattish with a faint longitudinal groove down the center, pitted (Fig. 17). Collections: 83 (0); representative: T. S. Brandegee 1139 (UC); M. Jones 511 (POM); C. Baker 549 (GH, NY, POM, RM, US); L. Higgins 2235, 2236, 2244, (BRY, WTS); A. Nelson 9812 (RM, UC); W. Weber 9416 (RSA, UC, UT); R. Hartman 2782 (BRY, RM).

Habitat.— Gravelly and sandy soils and talus slopes from 7,050 feet elevation upward to timberline. Commonly in open tundra and grassy alpine slopes of spruce, fir, pine, or aspen communities. Sometimes growing as a weed along roadsides and in waste field, July to September.

Distribution.— Mostly along or east of the Continental Divide in central and south central Colorado, south to Colfax Co., New Mexico (Map 5).

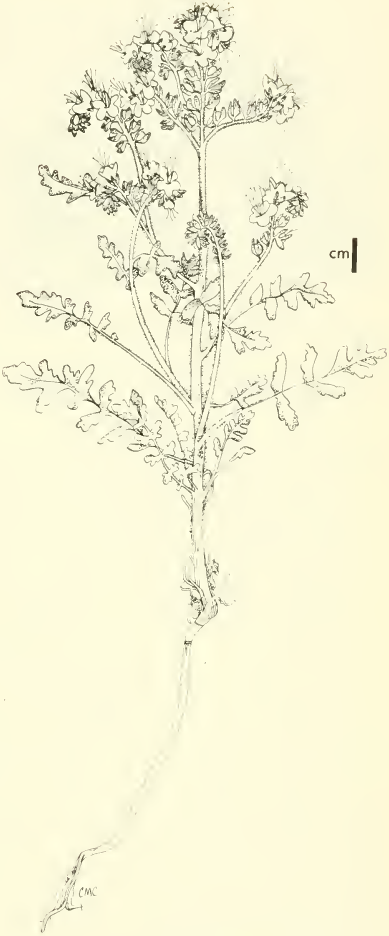


Fig. 16. *Phacelia bakeri* (Brand) Macbride. R. Hartman 2782 (BRY).

This taxon was misinterpreted by Brand (1913). The type specimen is the only material cited by him that belongs to *bakeri* in a strict sense. Macbride (1917) and Voss (1937) present additional information on Brand's treatment of this entity. *P. bakeri* is related to *P. glandulosa* Nutt., differing in the lack of excavations on the ventral surface of the seeds, usually greener herbage, later flowering time, and distribution.

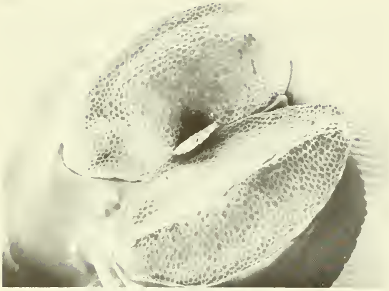


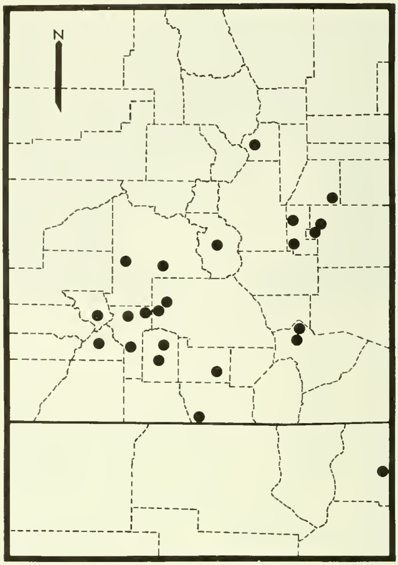
Fig. 17. Dorsal and ventral view of the seeds of *P. bakeri* (Brand) Macbride. C. Baker 549 (GH).

8. *Phacelia bombycina* Wooton & Standley Fig. 18

Phacelia bombycina Wooton & Standley. Contr. U.S. Natl. Herb. 16:163. 1913. Holotype: New Mexico: Carton Co.: on gravelly banks at Mangas Springs, March or April 1880, H. Rusby 276 (US!); Isotypes (NY, NY, UC, US). Paratypes: New Mexico: Grant Co.: Bear Mountains near Silver City, no date, C. Metcalfe 75 (NY, POM, UC, US, US).

Phacelia tenuipes Wooton & Standley. Contr. U.S. Natl. Herb. 16:163. 1913. Holotype: Carizalillo Spring, 17 April 1902, E. Mearns 91 (US!).

Annual 0.9-4.1 dm tall; stems 1-several, often branched throughout, erect and very brittle, setose to puberulent and glandular at least in the inflorescence; basal leaves petiolate (the petiole up to 5 cm long), oblong to nearly orbicular, pinnatifid into oblong to ovate, crenate lobes, setose and often glandular on both surfaces, 1.5-8 cm long, 0.5-2.5 cm wide, upper reduced, short petiolate, lobed; inflorescence paniculate, narrow, with a few branches; individual cymes with numerous, crowded flowers, pedicels short, stout, setose to puberulent and glandular; sepals oblong to elliptical, up to 3.5 mm long, setose to glandular; corolla blue to violet, 5-6 mm long and wide, campanulate, lobes pubescent; stamens exserted, anthers yellow, filaments bluish violet; style exserted, bifid to about the middle, pubescent below the middle, bluish violet; capsule 2.5-2.7 mm long and broad, globose, pilose and glandular especially at the apex; mature seeds oblong to elliptical, cymbiform, 2.2-2.5 mm long, 1-1.4 mm wide, dark brown, ventral surface pitted and divided by a prominent ridge, the ridge corrugated on one side, margins corrugated, lighter than the center, dorsal surface pitted (Fig. 19). Collections 89 (9); representative: L. Goodding 2230 (RM, UC); W. Cottam 10198 (UC); D. Demaree 42048 (UC); L. Higgins 2877 (BRY, WTS); H. Ripley and R. Barneby 4218 (RSA); D. Atwood 2195, 2241, 2256, 2280 (BRY); D. Atwood 2250, 2253, 2255 (BRY, CAS, NY, WTS).



Map 5. Southern Colorado and northern New Mexico. Distribution of *P. bakeri* (Brand) Macbride.

Habitat.— Sandy, gravelly, or lava slopes and mesas from an elevation of 1,500 to 7,500 feet. Commonly found in the *Larrea*, *Prosopis*, and other Lower Sonoran mixed shrub communities, late March to late May.

Distribution.— Sierra Co., New Mexico, southward to Chihuahua and Sonora, Mexico, westward through southern and central Arizona to Yavapai and Coconino cos. (Map 6).

The character differences that Wooton and Standley (1913) used to separate *P. tenuipes* and *P. bombycina* vary depending on the maturity of the plants

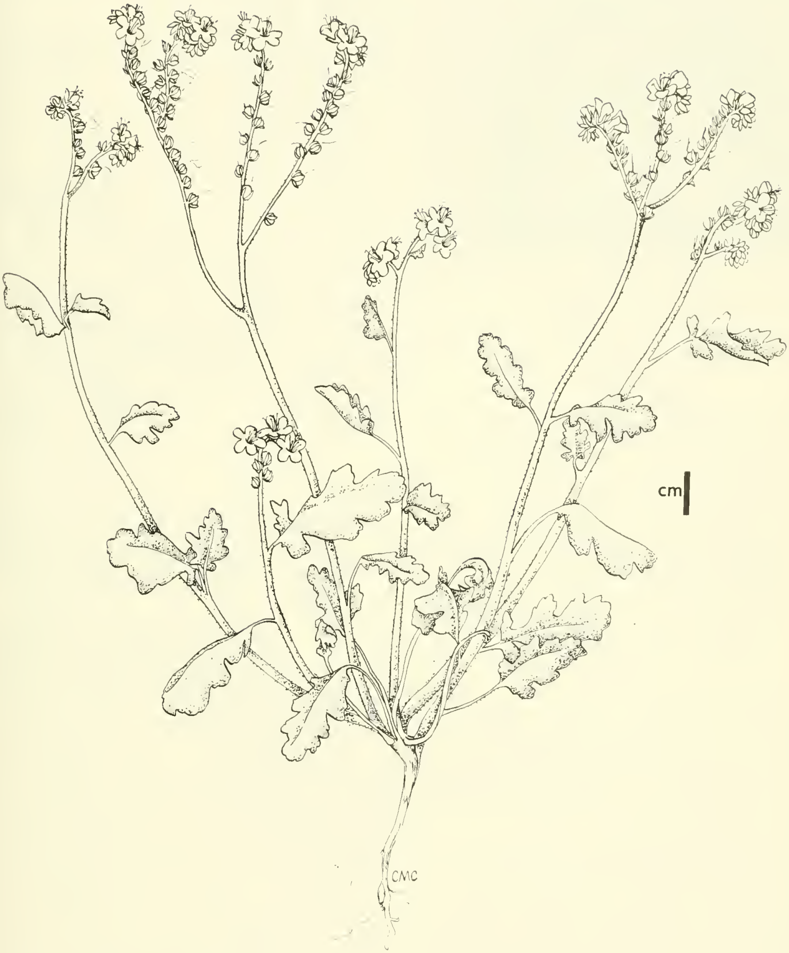


Fig. 18. *Phacelia bombycina* Wooton & Standley. D. Atwood 2253 (BRY).

and environmental conditions. Of the two taxa, the original description of the latter better fits the entity concerned. For these reasons *P. tenuipes* is placed in synonomy. The holotype data indicate that *P. bombycina* was collected in March and April; however, an isotype in the U.S. herbarium gives the exact data as 25 March 1880.

This entity has been confused with both *P. intermedia* and *P. crenulata*. It is readily distinguished from the former by the exserted stamens, larger blue lavender corollas, very brittle and less glandular stems, and smaller seeds. It differs from the latter by its brittle stems and smaller, darker seeds.

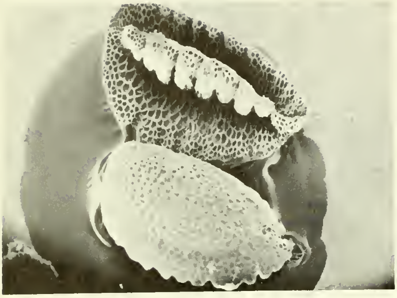


Fig. 19. Dorsal and ventral view of the seeds of *P. bombycina* Wooton & Standley. D. Atwood 2255 (BRY).

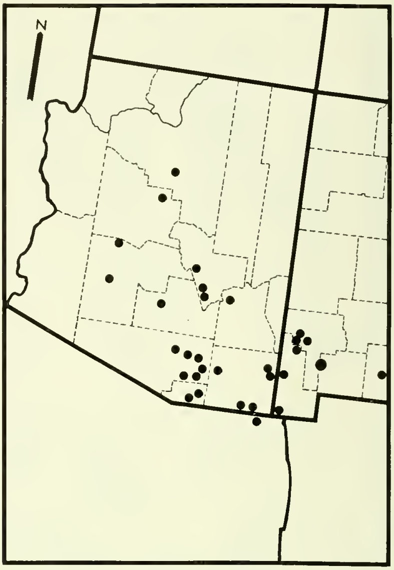
9. *Phacelia coerulea* Greene
Fig. 20

Phacelia coerulea Greene, Bull. Torr. Bot. Club 8:122. 1881. Lectotype: bluffs of the Gila (New Mexico), 23 April 1881, E. Greene s.n. (GH!).

Phacelia invenusta Gray, Proc. Amer. Acad. 20:303. 1885. Lectotype: Arizona: Pima Co.: Sierra Tucson, 12 April 1884, C. G. Pringle s.n. (GH!); duplicates (US), in part.

Phacelia intermedia Wooton, in part. Paratypes: New Mexico: Socorro Co.: San Antonio, Quitman Mountains, 14 March 1852, C. Wright 1579 (GH, GH, GH, NY); Texas: El Paso Co.: El Paso, March 1851, Thurber 11 (GH, GH, NY, NY).

Annual, 0.5-6 dm tall; stems erect, branched throughout, reddish, puberulent to setose and sparsely to densely stipitate-glandular, leafy throughout; leaves oblong to ovate, gradually reduced from the base upward, upper deeply sinuate, lower pinnatifid, dorsal surface with setose appressed hairs, dorsal surface setose to glandular, 0.6-8 cm long, 0.3-2.5 cm wide, petioles from 5 cm long at the base to nearly sessile at apex, margins crenate; inflorescence terminal, commonly loosely paniculate or cymose, setose, stipitate-glandular and puberulent; scorpioid cymes compact in flower but loosening in fruit, 1.5-7 cm long; flowers nearly sessile in flower to 1 mm long in fruit; corolla campanulate, lobes pale mauve to blue (turning white in fruit), tube yellowish, 3-4 mm long and broad, glabrous; sepals narrowly oblanceolate to elliptical, 2.5-4 mm wide, setose to brownish stipitate-glandular, 3/4 as long as the corolla, shorter or sometimes longer than the capsule; stamens mostly included to slightly exserted, anthers yellow, ovate, filaments bluish; style included to slightly exserted, equaling the stamens; capsule globose, 2.5-3.5 mm long, 1-1.8 mm wide; mature seeds dark brown, ventral surface pitted and divided by a prominent ridge, the ridge corrugated on one side, margins usually corrugated, dorsal surface pitted, 0.3-0.4 mm of the margin slightly elevated and smoother than the pitted center (Fig. 21). Collections: 112 (6); representative: M. Jones s.n. (POM); W. Wooton s.n. (NY); C. Parry 934 (NY); E. Greene s.n. (GH); C. Wright 1579 (GH, GH, GH, NY); D. Atwood 2137, 2152, 2196a, 2573 (BRY); D. Atwood 2197, 2281 (BRY, CAS, NY, WTS); L. Higgins 3126, 3134, 2978, 2999 (BRY, WTS).



Map 6. Southwestern New Mexico, Arizona, and adjacent Sonora, Mexico. Distribution of *P. bombycina* Wooton and Standley.

HABITAT.— Gravelly and arid calcareous hills and banks, sandy-gravelly stream beds, and rocky ledges from 2,000 to 6,000 feet. Commonly associated with the paloverde and creosote mixed shrub communities. Usually locally scattered, late February to early July.

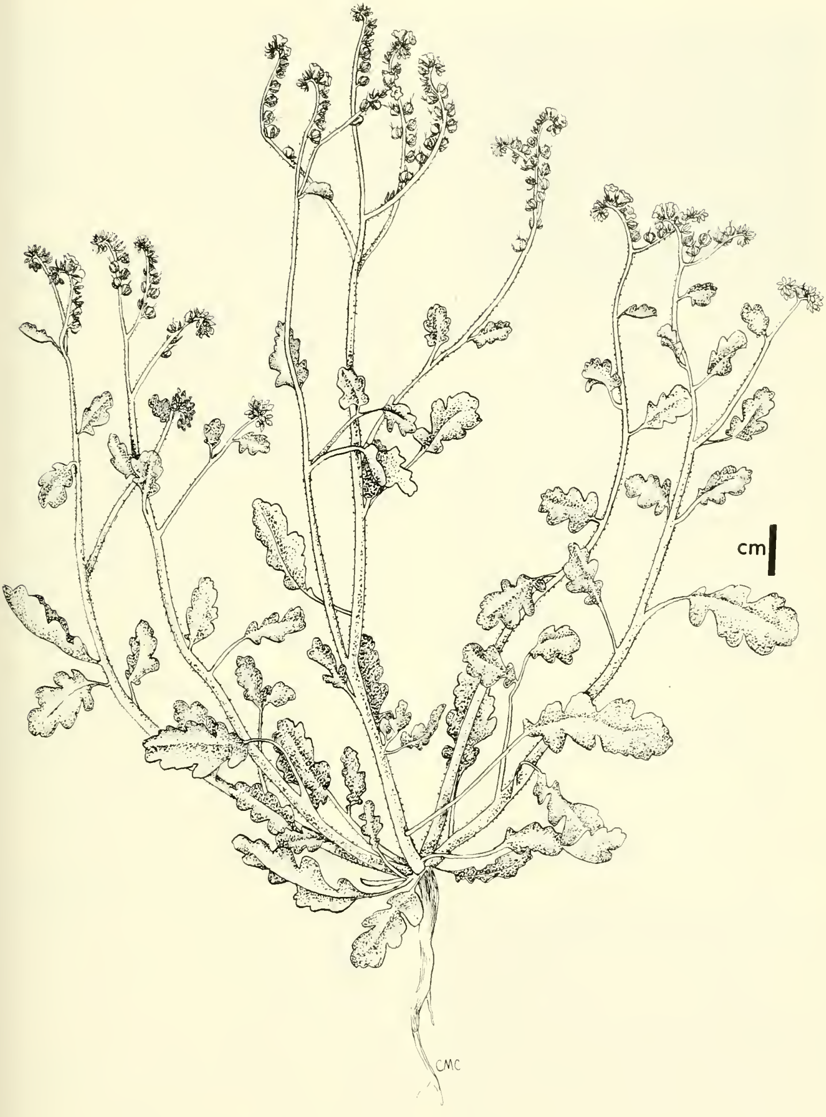


Fig. 20. *Phacelia coerulea* Greene. D. Atwood 2196a (BRY).

DISTRIBUTION.— Southern Nevada in Clark Co., southeastern California in San Bernardino Co., eastward through Mohave Co. to southern Arizona and southern New Mexico from Socorro and Lincoln cos. to El Paso, Presidio, and Brewster cos., Texas, and adjacent Mexico in the state of Chihuahua. Only one collection

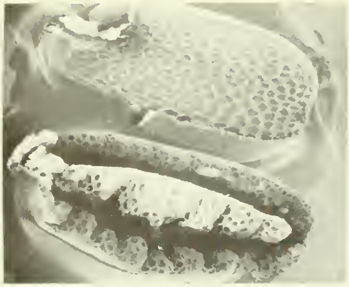
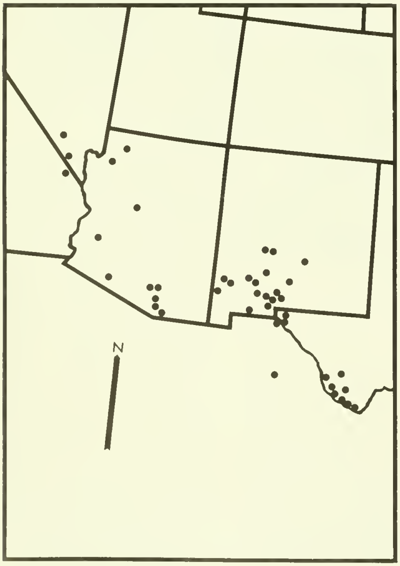


Fig. 21. Dorsal and ventral view of the seeds of *P. coerulea* Greene. H. Ripley and R. Barneby 3361 (CAS).

is known from Nevada and California (Map 7).

Greene cited no material on which he based his original description in November 1881. Voss (1937) noted this fact and selected Greene's collection at the Gray Herbarium as the type, since he had collected *P. coerulea* in the spring (23 April 1881) of the same year. However, Howell (1943), in Sertulum Greeneanum, indicates that a part of the type collection chosen by Voss is present in the Greene Herbarium at Notre Dame and that this specimen should be the type. Since Voss selected the specimen at the Gray Herbarium as the type, it should probably stand as such even though Greene's original is at Notre Dame.



Map 7. Southern Nevada, southeastern California, Arizona, New Mexico, western Texas, and adjacent Chihuahua, Mexico. Distribution of *P. coerulea* Greene.

This taxon is most closely related to *P. bombycina* and secondarily to *P. crenulata*. It differs from these species in its included stamens and smaller corollas. Jones (1908) contended that *P. coerulea* and *P. invenusta* Gray were separate species. The author believes, as did Gray (1886) and Voss (1937), that the latter is the same entity as the former. Howell (1941) reported *P. coerulea* from San Bernardino Co., California (H. Ripley and R. Barneby 3361 (CAS, RSA). To my knowledge this is the only collection from California.

No type was selected by Gray when he described *P. invenusta*; therefore I have selected the Pringle collection (GH) as the lectotype. Duplicates are located at CAS and a fragment at US.

10. *Phacelia congesta* Hooker
Fig. 22

Phacelia congesta Hooker. Bot. Mag. 62:t. 3452. 1835. Holotype: Texas: Galveston Co.: Galveston Bay. Drummond 303 (GH!).

Phacelia congesta Hooker var. *typica* Voss. Bull. Torr. Bot. Club 64:133. 1937. Torr. Bot. Club 64:133. 1937.

Phacelia congesta Hooker var. *dissecta* Gray. Syn. Fl. II:1 Suppl., 415. 1886. Holotype: Texas: Dallas Co.: shaded rocks, Dallas, May and July 1880, Reverchon s.n. (GH!); duplicates (CAS, GH, GH, NY, NY).

Phacelia dissecta (Gray) Small. Fl. Southeastern U.S. pp. 972, 1337. 1903.

Phacelia conferta D. Don. Gen. Syst. Gard. 4:397. 1837.

Erect, often robust, annual plants, 1-10 dm tall; stems simple or diffusely branched throughout, with multicellular stipitate glands and puberulent to hispid unicellular hairs; leaves oblong in outline, pinnately compound, the 3 terminal lobes usually not completely lobed to the midrib, often somewhat larger than the lower, usually petiolate lobes, 1-12 cm long, 0.5-4 cm wide, strigose and sometimes glandular; inflorescence of

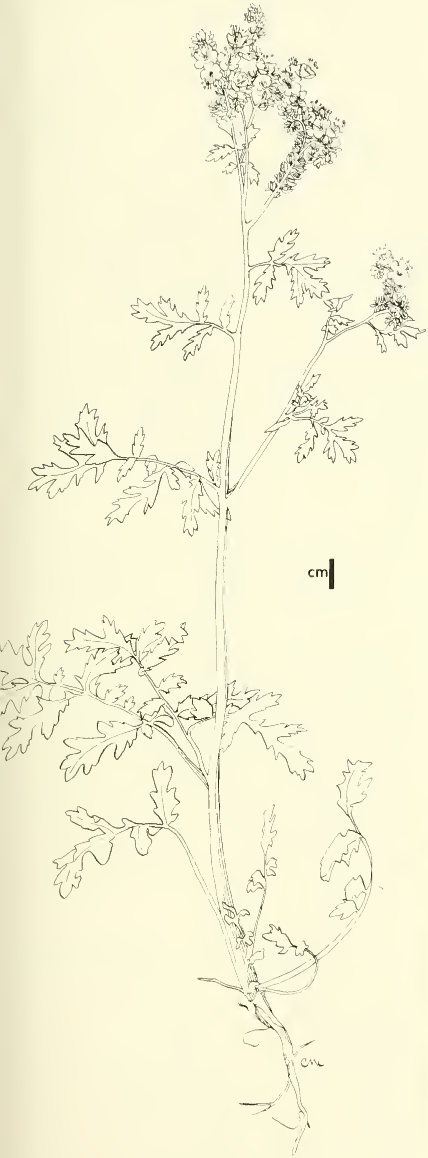


Fig. 22. *Phacelia congesta* Hooker. D. Atwood 2046 (BRY).

terminal, compound, scorpioid cymes, the individual cymes 1.5-15 cm long, pedicels 2.5 mm long or less, pubescent; sepals narrowly linear, 3-4.5 mm long, 0.5-0.7 mm wide, setose to hispid and often glandular; corolla campanulate, blue (rarely white), 4-6 mm long and wide, the lobes pubescent; stamens and style exserted, ca. 2-4 mm long, anthers pale yellow, filaments purplish; style 7-8 mm long, bifid 3/4 its length, lower 1/4 pubescent; capsule subglobose to oval, 2.3-3.6 mm long, 2.3-3 mm wide, puberulent and often glandular; mature seeds usually 4, sometimes 1 or 2, 2.6-3.2 mm long, 1.2-1.4 mm wide, elliptical to oblong, brown, reticulate to scabrous, ventral surface excavated on both sides of the ridge (Fig. 23). Collections: 222 (21); representative: V. Cory 28660 (GH); R. McVaugh 7780 (UC); E. Palmer 33743 (NY, US); H. Ripley and R. Barneby 11107 (CAS); E. Tyler s.n. (US); L. Higgins 2671, 3162 (BRY); D. Atwood 2048a, 2049, 2063, 2098, 2099, 2104-2107, 2111, 2117 (BRY).

Habitat.— Commonly associated with *Prosopis*, *Larrea*, *Acacia*, and *Opuntia* in sandy to sandy loam, rocky limestone, or sandstone flats and outcrops. Along the coast of southern Texas it grows on low shoreline dunes and is usually associated with *Quercus*, February to September, 300 to 7,000 feet.

Distribution.— Scattered throughout most of central and southern Texas, west to Eddy and Doña Ana cos., New Mexico; northeastern Mexico and Caddo and Com-

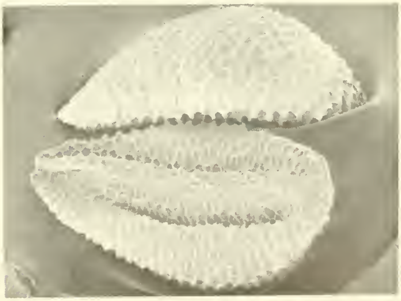


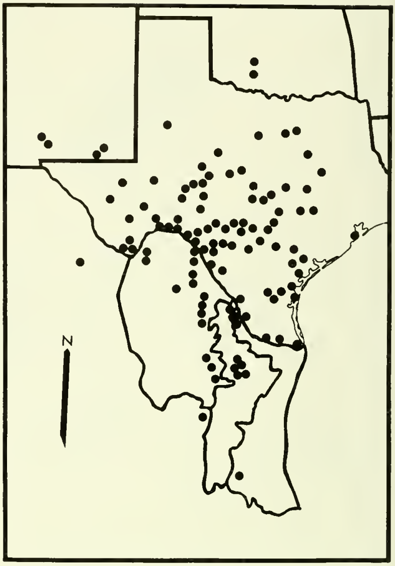
Fig. 23. Dorsal and ventral view of the seeds of *P. congesta* Hooker. D. Atwood 2117 (BRY).

manche cos., Oklahoma. Specimens from Florida, Massachusetts, and Sweden are presumably cultivated (Map 8).

Some plants from Tamaulipas, Zacatecas, and adjacent Nuevo León, Mexico, are fall-flowering and differ in sufficient morphological features to warrant further investigation. They are apparently rhizomatous perennials and possess a congested inflorescence and small, pale lavender flowers.

This taxon varies throughout its range in pubescence and in leaf size and shape. The number of seeds per capsule was used by former workers as an important character in separating var. *dissecta* from var. *congesta*. However, the author has examined capsules from the type material of var. *dissecta* and found that they possess 4 seeds. Other material examined varies in the number of seeds per capsule. This variation probably results from environmental conditions and is hardly consistent enough to warrant taxonomic recognition.

The seeds of *P. congesta* are dark when immature and are light brown upon reaching maturity. A more or less mottled pattern can be observed in the different stages of development.



Map 8. Texas, adjacent New Mexico, Oklahoma, and Mexico. Distribution of *P. congesta* Hooker.

11. *Phacelia constancei* Atwood
Fig. 24

Phacelia constancei Atwood. Rhodora 74(800): 451-454. 1972. Holotype: Arizona: Coconino Co.: 1 mi north of Fredonia, 27 May 1968, D. Atwood, 1385a (BRY!). Isotypes (ARIZ, BRY, CAS, NY, UC, US).

Erect biennial herb, 1.5-4.3 dm tall, leafy throughout; stems stout, simple or branched throughout, reddish, from hirsutulous to hirsute, and finely glandular; leaves mostly petiolate, 1-10 cm long, 0.3-1.5 cm wide, revolute, from undulate to pinnatifid, linear to lanceolate, upper surface hirsutulous with scattered glandular hairs; inflorescence of compound scorpioid cymes; pedicels to 1 mm long; sepals elliptic to oblanceolate, 3-4 mm long, hirsutulous to hirsute and stipitate-glandular; corolla tubular, whitish, 5-6 mm long; stamens exserted 3-4 mm; style bifid, lower 1/3 pubescent, exserted 3-4 mm longer than the stamens; capsule subglobose, glandular, and hirsutulous throughout, shorter than the sepals, mature seeds 4, black, 2.5-2.8 mm long, 1-1.2 mm wide, elliptic, the margins corrugated, ventral surface finely pitted, excavated, and divided by a prominent ridge, the ridge corrugated on one side, the dorsal surface finely pitted. Collections: 12 (10); representative: H. Ripley and R. Barneby 4836 (CAS, RSA); D. Atwood 1529 (BRY, GH, UC); D. Atwood 1785 (ARIZ, BRY, CAS, NY, UC, US, UTC); D. Atwood 1792b (BRY, CAS, GH, NY, POM, RM, US).

HABITAT.— Alkaline clay bluffs and flats of the Moenkopi formation, 5,500 feet. Late May to early August.

DISTRIBUTION.— Mohave Co., Arizona, and Kane Co., Utah (Map 9).

Taxonomically *P. constancei* appears to be most closely related to *P. palmeri* Torr. ex Wats. but is distinguished from that species by the smaller growth form, narrower and more revolute leaves, the reddish stems with shorter and fewer hairs, and the leafier lateral inflorescence branches.

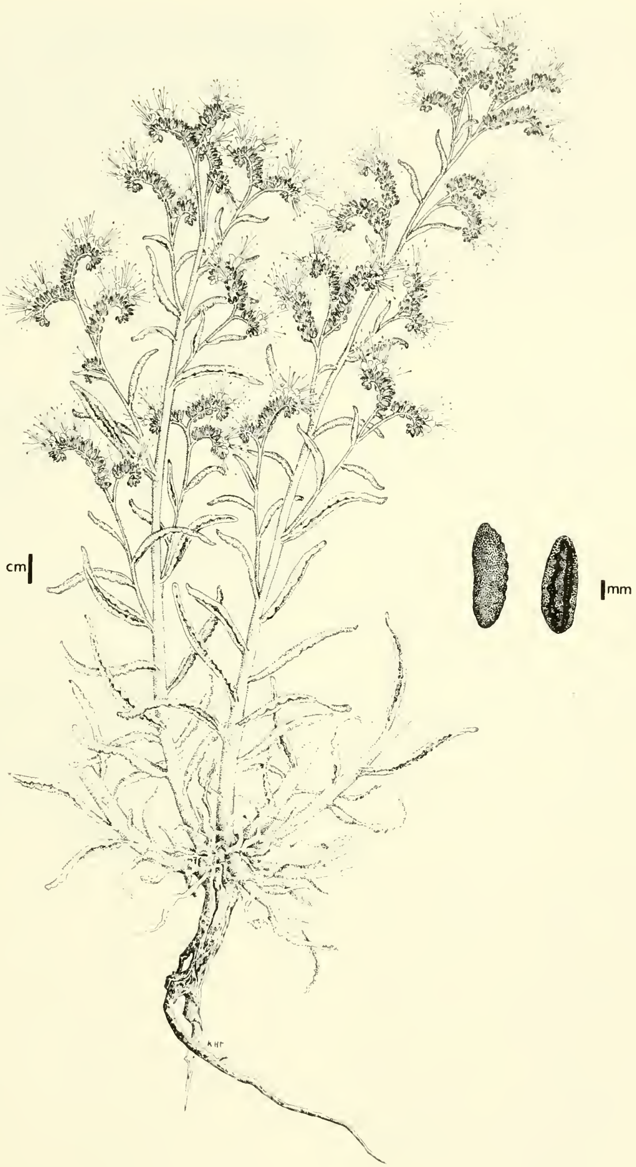
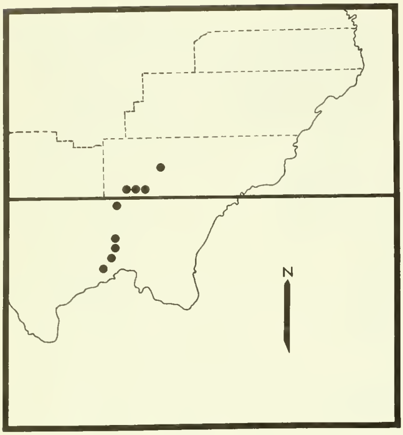


Fig. 24. *Phacelia constancei* Atwood. D. Atwood 1835a (BRY).



Map 9. Southern Utah and northern Arizona. Distribution of *P. constancei* Atwood.

12. *Phacelia corrugata* A. Nelson
Fig. 25

Phacelia corrugata A. Nelson, Bot. Gaz. 34:26. 1902. Holotype: Colorado: Garfield Co.: Rifle, 23 June 1900, G. E. Osterhout 2129 (RM!); Isotypes (NY, RM). Paratypes: Colorado: Mesa Co.: Palisades, 14 May 1898, C. S. Crandall 4174 (RM, RM, US).

Phacelia crenulata Torr. ex Wats. var. *corrugata* (A. Nels.) Brand, Das Pflanzenreich IV, 251:79. 1913.

Phacelia orbicularis Rydberg, Bull. Torr. Bot. Club 40:479. 1913. Holotype: Utah: Wayne Co.: Marvine Laccolite, 22 July 1894, M. Jones 4663 (US!).

Plants annual or winter annuals, 0.5-4.3 dm tall; stems greenish, from puberulent to finely stipitate-glandular and sometimes with a few longer hairs intermixed; leaves 1-10 cm long, setose to strigose and stipitate-glandular; sepals 4-5.5 mm long; corolla campanulate, deep blue, 6 mm long or more; stamens and style exserted over 3 mm, filaments and style blue; capsule elliptic, 3.8-4.5 mm long; mature seeds oblong to elliptic, light brown, 3.1-4 mm long, 1.3-1.7 mm wide, pitted, the ventral surface corrugated on the margins and one side of the ridge (Fig. 26). Collections: 216 (44); representative: R. Barneby 13033 (CAS, NY); C. Parry s.n. (CAS, UC); A. Eastwood and J. Howell 9358 (CAS, GH, UTC); L. Higgins 3304, 3303, 3305 (BRY, WTS); D. Atwood 1314, 1489, 1856, 2539, 2523, 2583, 2581, 2618 (BRY).

Habitat.— This species grows in a large number of habitats from dry, gravelly hillsides and flats, sandy soil, and red shaly clay to heavy clay soils. It grows with *Atriplex*, *Sarcobatus*, *Ephedra*, *Coleogyne* or grass, from 3,500 to 7,000 feet elevation. Late April to mid-July.

Distribution.— Eastern Nevada, eastward to Colorado from Garfield and Gun-

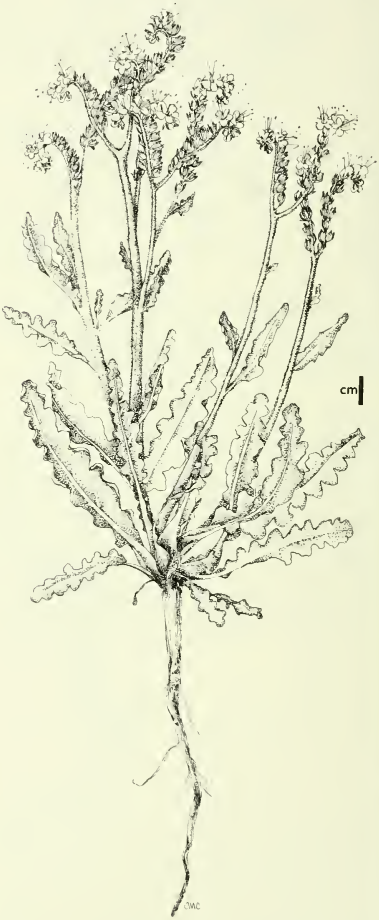


Fig. 25. *Phacelia corrugata* A. Nelson. D. Atwood 2457 (BRY).

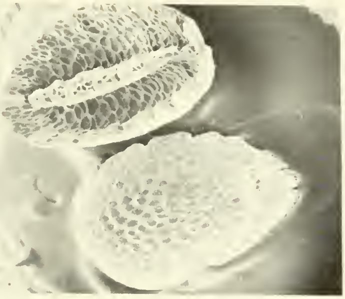
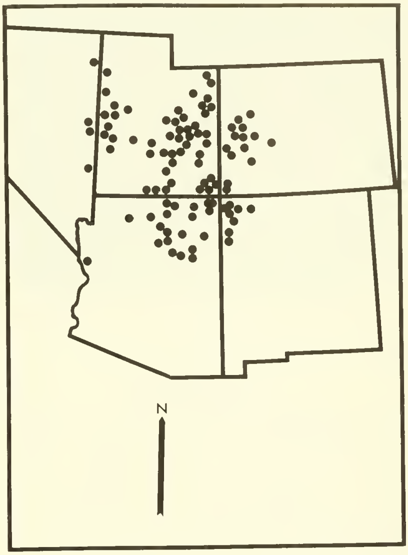


Fig. 26. Dorsal and ventral view of the seeds of *P. corrugata* A. Nelson. D. Atwood 2583 (BRY).

nison cos., southward through Ouray and Montezuma cos. to northwestern New Mexico and northern Arizona (Map 10).

This species is related to *P. crenulata* and apparently intergrades with it in eastern Nevada and western Utah. In general, however, it is easily distinguished from the latter by its greenish yellow stems, finer pubescence, and lighter, narrower seeds.



Map 10. New Mexico, Arizona, Colorado, Utah, and adjacent Nevada. Distribution of *P. corrugata* A. Nelson.

13. *Phacelia coulteri* Greenman

Phacelia coulteri Greenman. Proc. Amer. Acad. 41:241. 1904. Holotype: Mexico: state of Hidalgo: fields about Buena Vista Station, 4 August 1904, C. Pringle 8988 (GH!); Isotypes (CAS, MEXU, NY, NY, POM, UC, US, US). Paratypes: Mexico: Vera Cruz: Real del Monte, T. Coulter, no date 921 (?).

Phacelia neomexicana Thurber ex Torr. var. *coulteri* (Greenman) Brand. Das Pflanzenreich IV, 251:84. 1913.

Phacelia grandulosa Hem. Biol. Cent. Amer. Bot. 2:359. 1882.

Stout annual, 3.4-5.4 dm tall; stems solitary or branched, brownish to reddish, hirsute and provided with a softer indument; leaves pinnately compound, finely dissected, 0.2-1 dm long, 3-4.5 cm wide, hispid, with small dark glands, midrib and some of the lateral veins prominent ventrally and therefore producing a furrowlike appearance dorsally, the margins of the pinnae thick ventrally, lower leaves petiolate, the pedicels gradually reduced upward; inflorescence of terminal compound scorpioid cymes, hispid, with brownish glandular hairs, the cymes congested, up to 7 cm long, pedicels 1 mm long or less; sepals linear to oblanceolate, 3.3-3.6 mm long, 0.5-1.3 mm wide, hirsute and brownish glandular; corolla campanulate, bluish purple, 4-5 mm long and broad, finely pubescent petals barely fimbriate; stamens and style exserted 1-3.5 mm, the anthers yellow, filaments bluish; style ca. 6 mm long, bifid 1/2 its length, lower 1/2 glandular and puberulent; capsule oval, 2.4-3 mm long and broad, glandular and puberulent; mature seeds 4, oblong, brown, 1.6-1.9 mm long, 0.9-1 mm wide, pitted over the entire surface, the ridge level with the margins and deeply excavated on both sides (Fig. 27). Collections: 3 (0); representative: C. Pringle 8988 (CAS, GH, MEXU, NY, POM, UC, US); G. Rzedowski 16995 (MEXU); Linsley et al. 8 (UC).

HABITAT.— A weed of fields and roadsides as well as meadows and well-vegetated areas in the mountains, 7,350 to 8,500 feet. July to August.

DISTRIBUTION.— Known only from the states of Hidalgo and Zacatecas, Mexico.

Greenman did not select a holotype but Pringle 8988 was cited and is probably the type material.

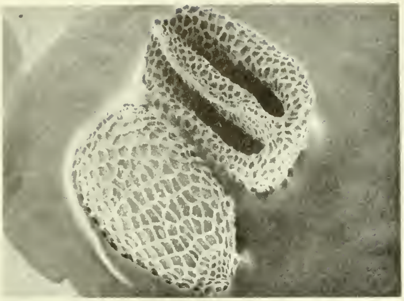


Fig. 27. Dorsal and ventral view of the seeds of *P. coulteri* Greenman. C. Pringle 8988 (MEXU).

Phacelia coulteri is related to *P. alba* but differs from that taxon in having smaller seeds (2 mm long) and larger campanulate corollas (4.5 mm long). The stamens and style are exserted up to 3.5 mm, the corolla lobes are only shallowly erose, and the leaves are more finely dissected.

14. *Phacelia crenulata* Torr. in Wats.

Plants annual, 0.25-8.3 dm tall; stems 1-several, simple to much branched, stipitate-glandular, setose or puberulent, reddish purple to green; leaves 0.4-1.2 dm long, 0.2-4.0 cm wide, strigose to setose and stipitate-glandular, sessile to petiolate; inflorescence of compound scorpioid cymes, setose and stipitate-glandular, the pedicels 0.5-2 mm long; sepals cleft to near the base, the lobes elliptic to oblanceolate, 3-3.5 mm long, 1-1.4 mm wide, glandular and setose; corolla campanulate to rotate-campanulate, violet, blue, or purple, pubescent, 4.5-10 mm long and broad; stamens and style exserted 5.5-11 mm; style bifid 3/4 its length, glandular below; capsule globose to subglobose, 2.6-4.1 mm long, 2-3 mm wide, puberulent and glandular; seeds 4, elliptic to oblong, 2-3.6 mm long, 1-2 mm wide, the dorsal surface with a dark center and lighter margins, the ventral surface corrugated.

14a. *Phacelia crenulata* var. *angustifolia* Atwood, var. nov.

Fig. 28

Phacelia crenulatae Torr. in Wats. var. *crenulatae* affinis sed brevioribus et ramosioribus, foliis angustioribus, corollis violaceis, staminibus et stylis excertis 5-6 mm, capsulis subglobosis 3-4 mm longis 2-3 mm latis, seminibus ellipticis 2-3 mm longis, 1-1.75 mm latis.

Annuals, 1.4-3.9 dm tall; stems simple to more commonly branched from the base, finely and densely stipitate-glandular, setose and puberulent, reddish purple especially below; leaves 1.1-9 cm long, 0.2-1 cm wide (up to 2.2 mm wide), stipitate-glandular and setose, petiolate; pedicels 1 mm long; corolla campanulate, violet, 7-10 mm long and broad; stamens and style exserted 5-6 mm; capsule subglobose, 3-4

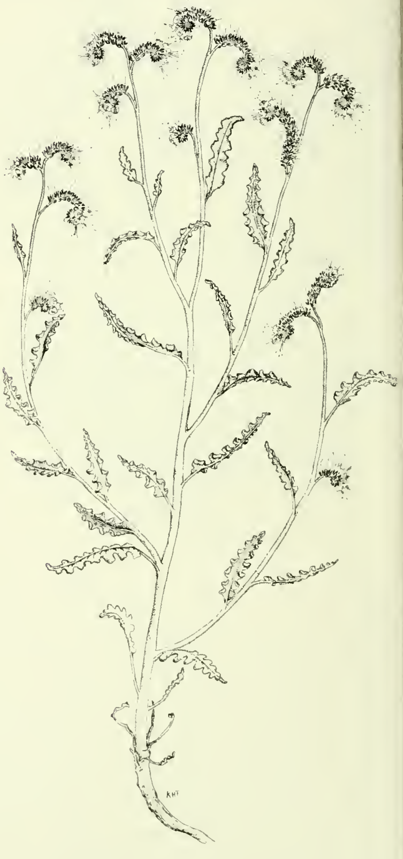


Fig. 28. *Phacelia crenulata* Torr. in Wats. var. *angustifolia* Atwood. Atwood 2523 (BRY).

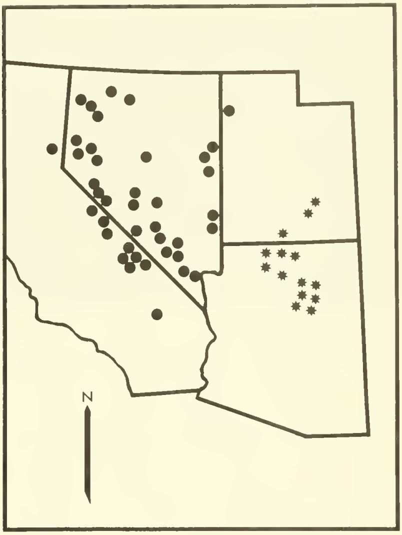
mm long, 2-3 mm wide; seeds 4, elliptic, 2-3 mm long, 1-1.75 mm wide.

Type.— Arizona: Coconino Co.: Small mesas just north of Wupatki National Monument Headquarters, sandy soil covered with volcanic ash, 18 May 1970, N.D. Atwood 2597 (Holotype: bry; Isotypes: to be distributed).

Additional materials examined: Arizona: Coconino Co.: D. Atwood 1784, 2602, 2600, 2606, 2604, 3650, 4559, 4555, 2597 (bry); L. Higgins 5187, 5396 (bry); L. Williams 5993 (bry); L. Cureton 45 (bry). Utah: Beaver Co.: D. Atwood and L. Higgins 3839 (bry). Garfield Co.: D. Atwood 1356 (bry). Kane Co.: D. Atwood 1532B, 3603, 3612 (bry); L. Higgins and D. Atwood 5247 (bry); R. Allen 211, 243 (bry).

Habitat.— Sandy, clay, or rocky ground in the canyons and benches below 5,000 feet elevation, April-June.

Distribution.— Coconino Co., Arizona, north to Kane, Garfield, and Beaver cos., Utah (Map 11).



Map 11. Utah, Nevada. Arizona, and California. Distribution of *P. crenulata* Torr. in Wats. var. *crenulata* ●; var. *augustifolia* ★.

14b. *Phacelia crenulata* var. *crenulata*

Phacelia crenulata Torr. in Wats., Bot. King Exped. 251. 1871. Holotype: Nevada: Pershing Co.: Trinity Mountains. May 1868, S. Watson 873 (ny!); duplicates (gh, us).

Phacelia crenulata Torr in Wats. var. *vulgaris* Brand, Das Pflanzenreich IV. 251:78. 1913.

Phacelia crenulata Torr. in Wats. var. *funerea* Voss in Munz, Man. So. Calif. Bot. 409, 600. 1935. Holotype: California: Mono Co.: Black Canyon, White Mountains, 12 May 1930, V. Duran 561 (pom!); Isotypes (b, cas, gh, ny, uc, us).

Plants annual, 0.25-8.3 dm tall; stems 1-several, simple or branched, puberulent, pilose, setose and stipitate-glandular, reddish purple to green; leaves 0.4-1.2 dm long, 0.5-4 cm wide, strigose to setose and stipitate-glandular, sessile to petiolate; inflorescence of compound scorpioid cymes, puberulent to setose and stipitate-glandular, the pedicels 0.5-2 mm long; sepals elliptic to oblanceolate, 3-5.3 mm long, 1-1.4 mm wide, setose and stipitate-glandular; corolla campanulate to rotate-campanulate, blue, pale purple, or violet, pubescent, 4.5-7 mm long and broad; stamens and style exserted 5.5-11 mm; style bifid 3/4 its length, glandular pubescent below; capsule globose to subglobose, 2.6-4.1 mm long, 2.3-3.2 mm wide, puberulent and glandular; seeds 4, elliptic to oblong, 2.8-3.6 mm long, 1.2-2 mm wide, the dorsal surface with a dark center and light margins, the ventral surface corrugated (Fig. 29). Collections: 124 (13): representative: Lemmon s.n. (us); C. Purpus 5976 (uc); J. Howell 26588 (cas); C. Purpus s.n. (uc); D. Atwood 2597, 2600, 2623

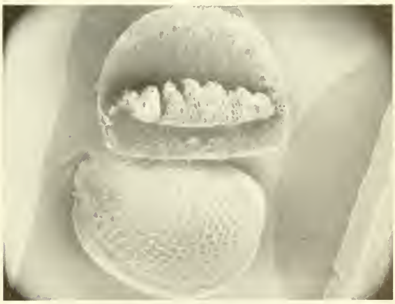


Fig. 29. Dorsal and ventral view of the seeds of *P. crenulata* Torr. in Wats. var. *crenulata*. D. Atwood 2623 (bry).

(BRY); P. Munz 14790 (CAS, POM); A. Nelson 3433 (RM).

HABITAT.— Rock slides, limestone talus, lava flows, gravelly and sandy soil of the foothills and canyons, from 4,600 to 8,000 feet elevation. Late February to early July.

DISTRIBUTION.— Nevada, eastward to western and southern Utah (except Washington Co.), and southward to Mohave and Coconino cos., Arizona, and eastern California from Nevada Co. southward to San Bernardino Co. (Map 11).

Phacelia crenulata was described from immature specimens (lacking seeds) in the northern part of its range in northwestern Nevada. This has resulted in some confusion as to its relationship to such other closely allied species as *P. corrugata* A. Nels. and *P. ambigua* Jones. Examination of specimens from Pershing Co., Nevada, as well as surrounding counties, reveals that *P. crenulata* is quite distinct from both *P. corrugata* and *P. ambigua*. However, there is some overlap in morphological characters where the species grow together. For the most part *P. crenulata* differs from *P. ambigua* in its reddish, usually simple and only slightly setose stems, and its distinctive seed characters. *P. corrugata* is easily distinguished by its yellowish green stems, uniformly fine-glandular pubescence, and distinctive seed.

The type of var. *funera* Voss appears to be morphologically the same as the type of *P. crenulata*. The author has been unable to study this complex in the field; when field observations and greenhouse studies have been accomplished, a change in taxonomic status may be necessary. However, until such studies are carried out, the present arrangement seems the most natural.

15. *Phacelia denticulata* Osterhout
Fig. 30

Phacelia denticulata Osterhout. Torreya 16:70. 1916. Holotype: Colorado: Larimer Co.: The Glades, Owl Canyon, between Fort Collins and Livermore, 18 June 1915, G. Osterhout 5233 (RM!); Isotypes (NY, RM, RM, RM).

Phacelia glandulosa Nutt. ssp. *eu-glandulosa* Brand var. *australis* Brand, Das Pflanzenreich IV. 251:82-83. 1913, in part. Lectotype: Colorado: El Paso Co.: Manitou, 15 July 1903, F.E. and F.S. Clements 47.1, in part (US!); duplicate (GH).

Phacelia neomexicana Thurber ex Torr. var. *microphylla* Brand, Das Pflanzenreich IV, 251:84. 1913. Lectotype: Colorado: Canyon, 18 July 1878, central Colorado, T. Brandegee s.n. (GH).

Annual plants, 0.5-5.4 dm tall; stems erect, simple or sometimes branched, setose and stipitate-glandular; leaves oblong to oblanceolate in outline, pinnately cleft or divided, 1-7.5 cm long, 0.5-4.5 cm wide,

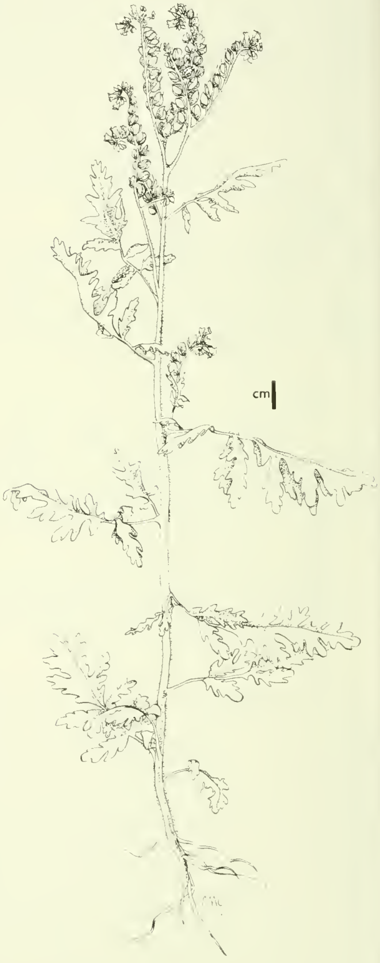
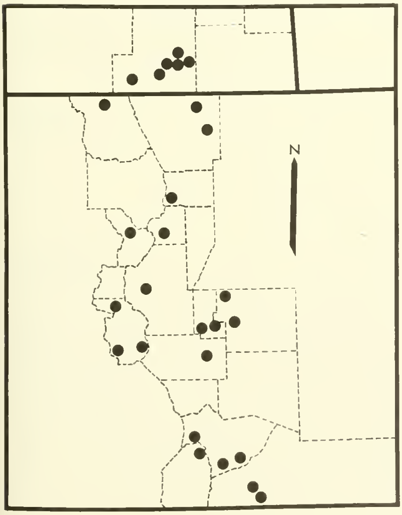


Fig. 30. *Phacelia denticulata* Osterhout. J. Ewan 18154 (UC).

strigose and stipitate-glandular; inflorescence of terminal scorpioid cymes, the longer cymes becoming 10 cm long in fruit; sepals narrowly linear to oblanceolate, 2.5 mm long in flower, 5-6 mm long in fruit, 0.8-0.9 mm wide, setose and stipitate-glandular; corolla tubular, light blue, 3.5-4.5 mm long, 2.3 mm wide, the lobes short, denticulate; stamens included; style included, bifid, glandular at base; capsule ovoid, 5 mm long, 3-3.5 mm wide, pilose and glandular; mature seeds 4, elliptical to oblong, brown, 4 mm long, 1.7 mm wide, ventral surface slightly excavated on each side of the curved ridge, alveolate, dorsal surface alveolate (Fig. 31). Collections: 61 (7); representative: H. Ripley and R. Barneby 7525 (CAS, NY); W. Weber 5974 (CAS); C. Shear 3306 (NY); A. Nelson 1361 (RM); D. Atwood 1941, 1946, 1959, 1973 (BRY).

HABITAT.— Gravelly, sandy, or clay banks, draws and flats of the prairie to higher mountain slopes from 6,800 to 9,700 feet. Commonly as understory of *Quercus*, *Cercocarpus*, *Artemisia*, and *Pinus edulis*. Frequently associated with *Populus tremuloides* and *Pseudotsuga* at the higher elevations, June to September.



Map 12. Colorado and southern Wyoming. Distribution of *P. denticulata* Osterhout.

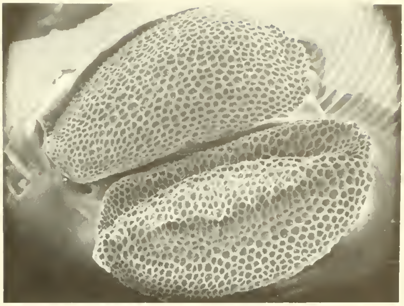


Fig. 31. Dorsal and ventral view of the seeds of *P. denticulata* Osterhout. D. Atwood 1973 (BRY).

DISTRIBUTION.— Albany and Laramie cos., Wyoming, southward through central Colorado (Map 12).

Phacelia denticulata is most closely related to *P. neomexicana*, from which it differes in having included stamens, a denser glandular pubescence, larger seeds, and a more robust, erect habit.

The holotype of *P. neomexicana* var. *microphylla* Brand was deposited in the Berlin Herbarium (Brand 1913). The author has seen the entire collection of the Crenulatae group at Berlin. Apparently most of their collection was destroyed during the war. This has made it necessary to select a lectotype for var. *microphylla;* the author has chosen the Brandegee collection at GH as the lectotype. Brand (1913) failed to select a holotype for *P. neomexicana* var. *australis*. Most of the material cited by him belongs to *P. bakeri* (Purpus 838, Baker 549, and Clements 47.1, in part). The Clements collection consists of several sheets, most of which are *P. bakeri*. However, the Clements collection at the U.S. National Herbarium and Gray Herbarium includes the only sheets which represent var. *australis*. I designate the specimen at the U.S. National Herbarium as the lectotype.

16. *Phacelia formosula* Osterhout
Fig. 32

Phacelia formosula Osterhout. Bull. Torr. Bot. Club 46:54. 1919. Holotype: Colorado: Jackson Co.: North Park near Waldren, along the road descending to Michigan Creek, 6 August 1918, G. Osterhout 5794 (RM!); Isotypes: (RM, RM, RM).

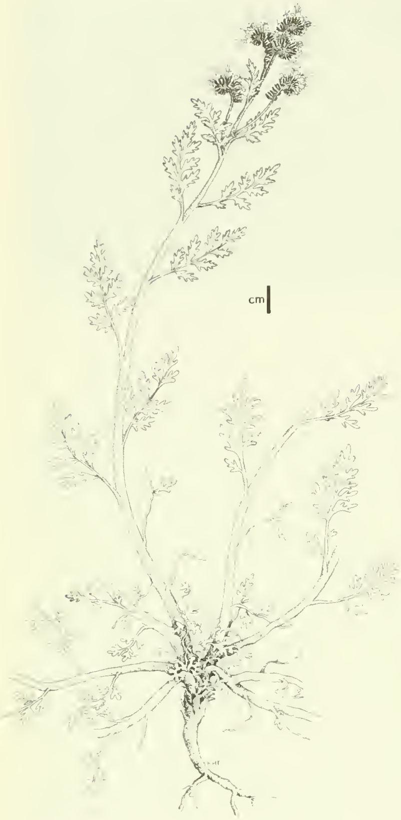


Fig. 32. *Phacelia formosula* Osterhout. D. Atwood 1971 (BRY).

Annual, 1.5-2.2 dm high, up to 3 dm broad; stems single or branched throughout (especially at base), glandular and hirsute, somewhat grayish; leaves lanceolate or elliptical, 3-7 cm long (up to 4.5), 1-3 cm wide, pinnately divided, strigose, hirsute and glandular; inflorescence of compound scorpioid cymes, cymes up to 5 cm long in fruit, and more densely glandular than the stems; sepals 3.2-3.8 mm long, 0.5-0.8 mm wide, glandular and hirsute; corolla campanulate, violet, 6 mm long, 6 mm wide, slightly glandular and pilose; stamens and style long exserted; style ca. 2 mm longer than the stamens and puberulent throughout; capsule oblong to oval, 3.5 mm long, glandular and hirsute; mature seeds 4, oblong, dark brown, 2.5-3 mm long, 1.2-1.4 mm wide, excavated ventrally on each side of the ridge, pitted, dorsal surface pitted, margins rounded and smooth. Collections: 7 (2); representative: D. Keck 889 (CAS, UC); H. Ripley and R. Barneby 9008 (CAS); D. Atwood 1977, 1977a (BRY).

HABITAT.— Loose sandy soil of sandstone bluffs at an elevation of 8,300 feet. Associated with *Artemisia* and *Tetradymia*, July to August.

DISTRIBUTION.— Apparently confined to Jackson Co., Colorado.

This species appears to be most closely related to *P. glandulosa* Nutt. but can be distinguished from that species by its usually much-branched, erect to spreading habit, less exserted stamens and style, darker seeds, narrower calyx lobes, and more pubescent style. *P. glandulosa* is a somewhat variable species, and *P. formosula* may, perhaps, best be treated as a variety of it; however, additional materials and field work are necessary before this suggestion can be confirmed.

17. *Phacelia glandulosa* Nutt.

Fig. 33

Phacelia glandulosa Nutt., Journ. Acad. Phil. n. ser. 1:160. 1848. Holotype: Wyoming: Lincoln Co.: about Ham's Fork, Colorado, of the West, July, T. Nuttall 93 (GH?).

Eutoca glandulosa (Nutt.) Hook., Kew Journ. Bot. 3:293. 1851. Wyoming: Sweetwater Co.: Greenriver. 31 May 1897, A. Nelson 3050 (RM!); Isotypes (GH, NY, RM).

Phacelia glandulosa Nutt. subsp. *eu-glandulosa* Brand var. *deserta* Brand.

Das Pflanzenreich IV, 251.82. 1913.

Plants annual or possibly biennial, 0.6-3.6 dm tall; stems simple or branched, erect, densely stipitate-glandular and hirsute; leaves lanceolate to oblong in outline, pinnatifid, 1-7 cm long, 0.5-3 mm wide, glandular and densely hirsute, the lower petiolate, the upper subsessile; inflorescence of congested terminal compound scorpioid cymes, stipitate-glandular and hirsute, 1-1.5 mm long, cymes elongating to 6.5 cm in fruit; sepals elliptical to oblanceolate, 3-4 mm long, 1.2-1.4 mm wide; corolla campanulate, purple to bluish, 5-7 mm long and broad, the lobes pubescent and often more or less crenate; stamens and style exserted 5-9

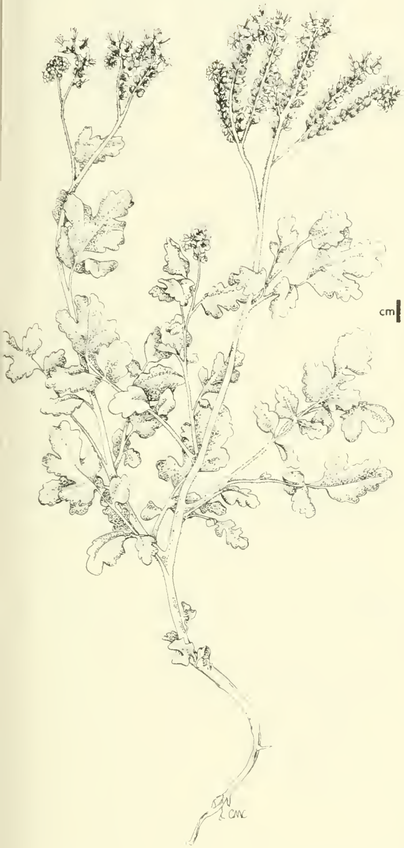


Fig. 33. *Phacelia glandulosa* Nutt. Hitchcock 10804 (UC).

mm, the style bifid 3/4 its length, the lower 1/4 pubescent; capsule subglobose, 3.5-4 mm long, 3.2-3.3 mm wide, glandular and setose; mature seeds elliptic to oblong, reddish brown, 2.4-3.3 mm long, 1.1-1.4 mm wide, pitted, the ventral surface excavated on both sides of the ridge (Fig. 34). Collections: 25 (1); representative: E. Graham 9774 (CAS, US); R. Davis 585 (US); H. Ripley and R. Barneby 8826 (CAS, NY); S. Watson 281 (GH, US); A. Rudvalis 70 (BRY); H. Fitch s.n. (CAS, NY, POM); A. Williams s.n. (NY).

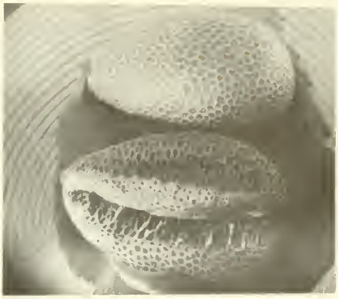


Fig. 34. Dorsal and ventral view of the seeds of *P. glandulosa* Nuttall.

HABITAT.— Rock slides, sandy talus slopes, and clay knolls from 5,000 to 7,050 feet. Mid-June to early August.

DISTRIBUTION.— West of the Continental Divide in Rio Blanco Co., Colorado, northward to southwestern and western Wyoming, southwestern Montana, and central Idaho in Lemhi and Custer cos. (Map 13).

For a discussion of this taxon see *P. formosula*.

18. *Phacelia howelliana* Atwood
Fig. 35

Phacelia howelliana Atwood. Rhodora 74(800): 456-462. 1972. Holotype: Utah: San Juan Co.: ca. 0.4 mi north of Bluff on Utah highway 163, in mouth of canyon, 13 May 1970, D. Atwood 2454 (BRY); Isotypes (ARIZ, ASC, B, BRY, CAS, GH, NY, UC, US, UTC).

Plants annual, 0.9-2.3 dm tall; stems mostly branched and leafy toward the base, glandular and hirsute; leaves broadly oblong to oval, 2.0-6.0 cm long, 1.0-2.5 cm wide, irregularly crenate to lobed, strigose and slightly glandular, the petiole up to 5 cm long; inflorescence of compound scorpioid cymes; pedicels up to 2 mm long; sepals linear to narrowly oblanceolate, 3.5-4.5 mm long, 1.0-1.2 mm wide, glandular and hirsute; corolla 5-6 mm long, 6-7 mm wide, rotate to funnelform, the lobes light violet to blue, the tube white; stamens and style exserted 3-4 mm, style shorter than the stamens, bifid 3/4 its length, lower 1/4 pubescent; capsule oblong to subglobose, glandular and hirsutulous, especially toward the apex; seeds 4, brown, 3.2-4 mm

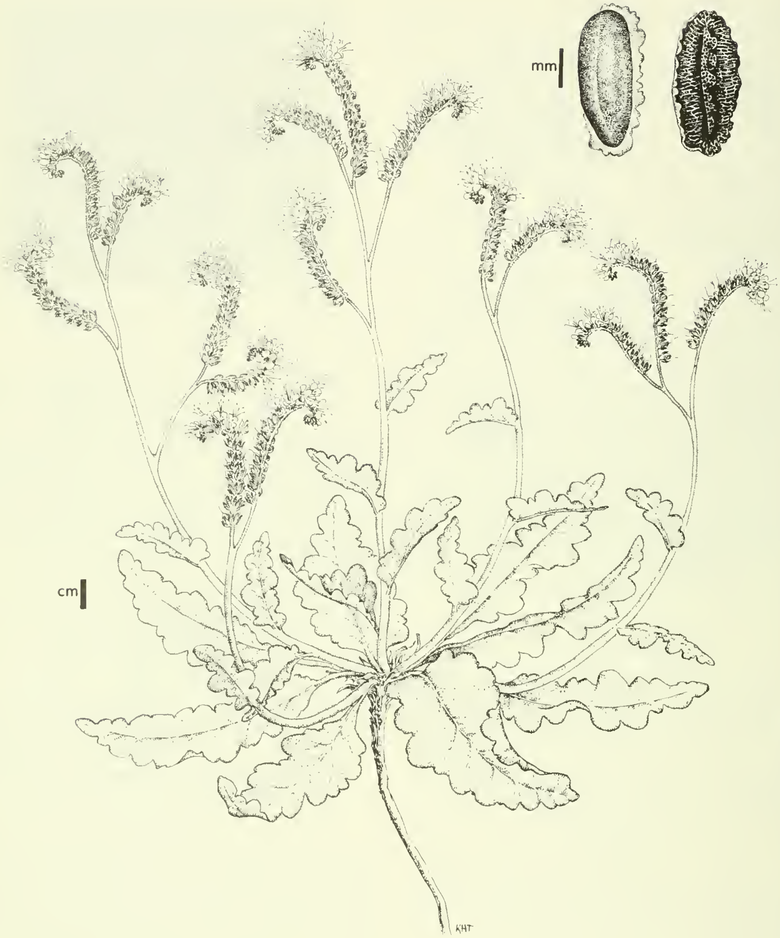
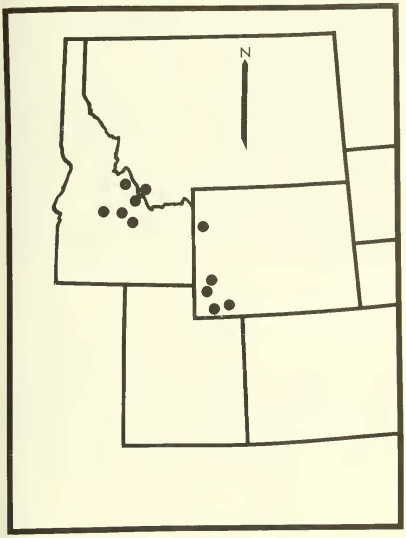


Fig. 35. *Phacelia howelliana* Atwood. D. Atwood 2454 (bry).

long, 1.4-1.8 mm wide, elliptical, the margins corrugated, involute to flattened, ventral surface pitted, excavated, and divided by a prominent ridge, the ridge sometimes curved to one side and barely corrugated, dorsal surface reddish brown, smooth and surrounded by a lighter margin (Fig. 36). Collections: 16 (3); representative: S. Welsh, D. Atwood and G. Moore 9957 (bry); A. Eastwood s.n. (ny); B. Harrison 11244 (bry); C. Hansen 101 (bry); M. Jones s.n. (pom); D. Atwood 2511 (ariz, asc, b, bry, cas, dixie, gh, jeps, ny, pom, rm, rsa, uc, us, ut, utc, wsc); J. Howell 24689 (cas).

Habitat.— Red sandy, gravelly, or clay soils at ca. 4,500 to 5,000 feet.

Distribution.— Known only from San Juan and Grand cos., Utah. It probably grows in Colorado near Moab and also



Map 13. Idaho, Montana, Wyoming, and Utah. Distribution of *P. glandulosa* Nuttall.

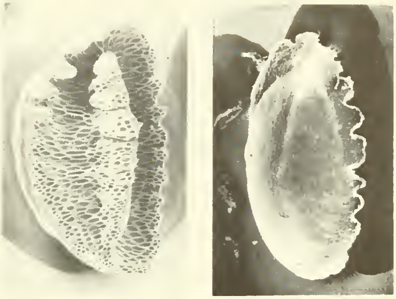


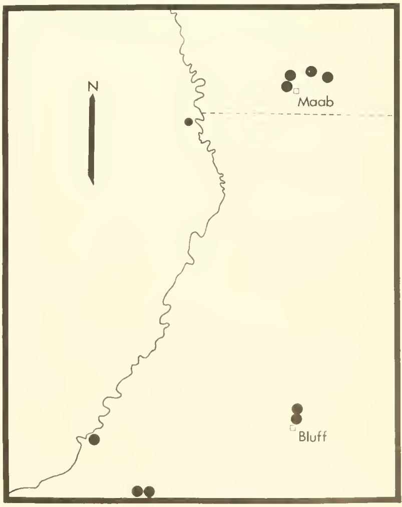
Fig. 36. Dorsal and ventral view of the seeds of *P. howelliana* Atwood. J. T. Howell 24687 (CAS).

Monument Valley in Arizona, although no specimens have been seen from either area (Map 14).

This entity is related to *P. corrugata* A. Nelson which grows throughout most of Utah and extends to Colorado, northern New Mexico, and northern Arizona. It is distinguished from *P. corrugata* by its low, much-branched growth form and smaller corolla with a white tube. The leaves are mostly basal, and the seeds are larger and reddish brown.

19. *Phacelia integrifolia* Torr. ex Watson

Plants annual (possibly biennial in var. *texana*), 1.2-6 dm tall, stems stout, green to reddish brown, simple or branched, puberulent, stipitate-glandular and hirsute; leaves simple, crenate to somewhat cleft, oblong to ovate or lanceolate, strigose, finely glandular, setose, lower leaves long petiolate, the upper short petiolate to sessile; inflorescence of compound scorpioid cymes, the cymes elongating to as much as 2.1 dm in fruit, pedicels 0.5-2 mm long; sepals elliptical to oblanceolate, 2.5-6.5 mm long, 0.9-2.8 mm wide, often reddish, puberulent, hirsute and stipitate-glandular; corolla campanulate, purplish to lavender, 4.5-6.5 mm long and broad, the lobes crenulate, pubescent; stamens and style exserted 4-6.5 mm; style bifid 2/3-3/4 its length, pubescent below, the filaments purplish, the stamens bluish green; capsule ovoid to globose, 2.6-5.3 mm long, 1.1-3.5 mm wide, glandular and puberulent; mature seeds ovate or elliptic to oblong, reddish brown or dark brown to black, 2.4-4.5 mm long, 1.3-2.2 mm wide, the dorsal surface pitted and transversely ridged, the margins more finely pitted than the



Map 14. San Juan and Grand counties, Utah. Distribution of *P. howelliana* Atwood.

excavated portions (these tending to have transversely elongate pits), the ventral surface excavated on both sides of the ridge, corrugated or corrugations lacking.

Key to the varieties of *P. integrifolia*

1a. Mature seeds 3 mm long or less, 1.4 mm wide or less, ventrally corrugated; capsule 3.1 mm long or less; plants of southeastern New Mexico and adjacent Texas .... var. *texana*

1b. Mature seeds 3.1 mm long or more, 1.7 mm wide or more, ventral corrugations lacking; capsule 3.2 mm long or more; plants widespread in rocky to sandy soil .... var. *integrifolia*

19a. var. *integrifolia*
Fig. 37

Phacelia integrifolia Torr. in Wats., Ann. Lyc. New York 2:222, t. 3. 1826. Holotype: on the Platte, 25 June 1820, Dr. James s.n. (NY!). *Phacelia arenicola* Brandegee. Univ. Calif. Pub. Bot. 4:185. 1911. Holotype: Mexico: Coahuila: El Toro near Movano. July 1910, C. A. Purpus 4458 (US!).

Phacelia integrifolia Torr. in Wats. var. *arenicola* (Brandegee) Brand. Das Pflanzenreich IV, 251:82. 1913.

Plants annual, 1.6-6 dm tall; stems puberulent, finely to densely stipitate-glandular and hirsute; leaves 1-13 cm long, 0.5-3 cm wide; cymes elongating to 2.1 cm in fruit, pedicels 1 mm long; sepals oblanceolate to elliptic, 3.5-4.5 mm long (4.4-6.5 mm in fruit), 1-1.8 mm wide (1.1-2.8 mm in fruit); corolla 5-6.5 mm long and broad; stamens and style exserted 5-6 mm; capsule ovoid to globose, 3.2-5.3 mm long, 3-3.5 mm wide; mature seeds oblong to elliptic, dark brown to black, 3.1-4.5 mm long, 1.7-2.2 mm wide, transverse ridges on the dorsal surface quite distinct, the ventral surface lacking corrugations, the ridge often curved to one side (Fig. 38). Collections: 113 (23); representative: L. Higgins 3138, 3129, 3131 (BRY); D. Atwood 2555, 2556, 2278, 2275, 2273, 2169 (B, BRY, CAS, NY, WTS); D. Atwood 2265, 2263, 2557a, 2274, 2171 (BRY).

HABITAT.— Sandy hills and flats, rocky hillsides of *Larrea*, *Yucca*, *Quercus*, *Coleogyne*, and grass communities. From 3,750 to 7,500 feet, late March to mid-September.

DISTRIBUTION.— Southeastern Utah in Kane and San Juan cos., southward through northeastern Arizona, eastward through much of New Mexico to western Texas and Chihuahua, Mexico (Map 15).

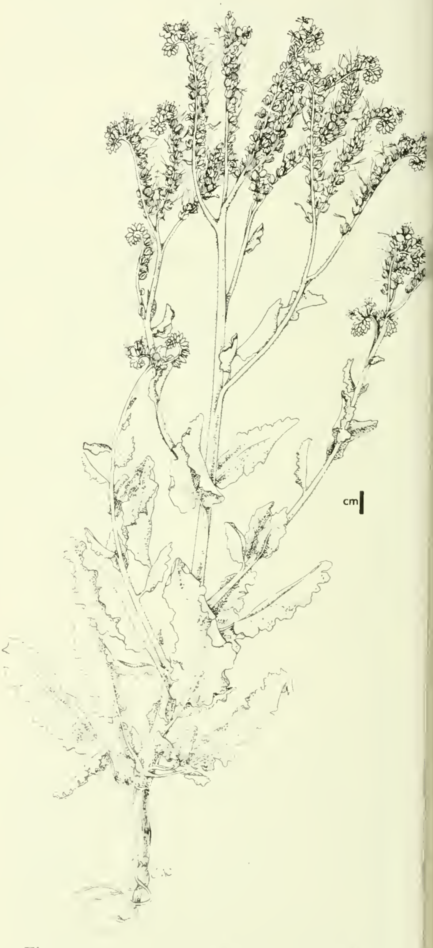


Fig. 37. *Phacelia integrifolia* Torr. ex Wats. var. *integrifolia*. L. Higgins 3131 (BRY).

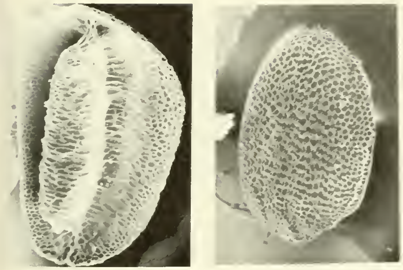
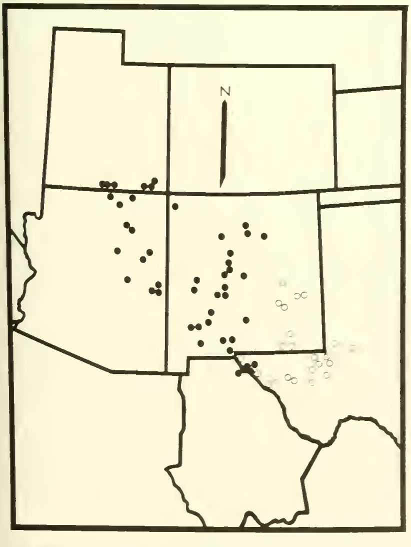


Fig. 38. Dorsal and ventral view of the seeds of *P. integrifolia* Torr. ex Wats. var. *integrifolia*. D. Atwood 2556 (BRY).

Considerable confusion has existed as to the relationships of this taxon to other species. This has probably resulted from the inadequate type material and initial misunderstandings that have been perpetuated and even enlarged upon by subsequent authors, Brand (1913) and Voss (1937). These misunderstandings have, in part, come about through lack of field work and by the fact that the corollas in most herbarium specimens fade to white and appear to be tubular. Var. *integrifolia* has a broad distribution and is easily distinguished by its large, broad, noncorrugated seeds. Plants from the higher elevations in western New Mexico and eastern Arizona are different morphologically. Additional field work is necessary to decide whether these differences are sufficient to warrant taxonomic recognition.



Map 15. Parts of southwestern United States and adjacent Mexico. Distribution of *P. integrifolia* Torr. ex Wats.: ● var. *integrifolia*; var. ○ *texana*.

19b. var. *texana* (Voss) Atwood, new comb.

Phacelia texana Voss. Bull. Torr. Bot. Club 64:141. 1937. Holotype: Texas: Hudspeth Co.: Finlay, 5 May 1931, M. E. Jones 28500 (POM!); Isotypes (RM, UC); photo at (BRY, NY, UC, US).

Plants annual or possibly biennial, 1.2-4.3 dm tall; stems puberulent, densely covered with short stipitate glands (usually 0.2 mm long or less) and sometimes with a few scattered longer, simple hairs; leaves 1-10 cm long, 0.3-2 cm wide, stipitate-glandular (0.2 mm long or less), and puberulent; cymes elongating to 1.4 dm in fruit, pedicels 0.5-1.2 mm long; sepals elliptical to oblanceolate, more or less heteromorphic (two narrow and three broad), 2.5-3 mm long (3.5-5.5 in fruit), 0.9-1.4 mm wide (1.2-2 in fruit) puberulent, stipitate-glandular, and setose; corolla 4.5-6 mm long and broad; stamens and style exserted 4-6.5 mm; capsule globose, 2.6-3.2 mm long, 1.1-2.6 mm wide; mature seeds ovate, reddish brown, 2.4-3 mm long, 1.1-1.4 mm wide, transverse ridges on the dorsal surface only fairly distinct, the ventral surface corrugated on the ridge and part of the margin. Collections: 38 (0); representative: C. Cory 37574 (UC); H. Wilkens 2209 (UC); L. Higgins 3157 (BRY, WTS); T. Collins 1182 (UC); U. Waterfall 4558 (GH, CAS, NY); R. McVaugh 8163 (UC).

HABITAT.— Gypsum, limestone, and calcareous soils in mixed shrub communities. Commonly associated with *Larrea*, *Foquieria*, and *Acacia*. 2,550 to 6,850 feet elevation. Late April to early October.

DISTRIBUTION.— Southeastern New Mexico and adjacent Texas (Map 15).

Var. *texana* differs morphologically from var. *integrifolia* in seeds and size of capsule. The corollas of var. *texana* appear to be lavender in contrast to the purplish corollas of the latter. Jones (1931) indicated that he had collected the type at Findlay, correctly spelled Finlay. The correct collection number is 28500 rather than 285ae as cited by Voss (1937).

20. *Phacelia intermedia* Wooton

Fig. 39

Phacelia intermedia Wooton. Bull. Torr. Bot. Club 25:457. 1898. Holotype: New Mexico: Doña Ana Co.: mesa west of the Organ Mountains, 10 April 1893, E. O. Wooton (US!); duplicates (UC, US).

Plants annual, 0.6-3.6 dm tall, stems simple or branched, often reddish, puberulent with short stipitate glands; leaves narrowly oblong, elliptic to ovate-lanceolate, sinuate to deeply lobed or pinnatifid, 0.5-8 cm long, strigose and stipitate-glandular or glandular, petiolate to sessile above; inflorescence of compound scorpioid cymes, terminal on the main stem and lateral branches, the cymes up to 1.5 dm long in fruit, pedicels subsessile to 1 mm long in flower, slightly longer in fruit; sepals linear to oblanceolate, 2.5-3.7 mm long, 1.3-1.5 mm wide, setose and glandular; corolla bluish violet, 6 mm long or less, campanulate, pubescent, the lobes crenate to entire; stamens and style exserted 3 mm or less, filaments violet, anthers yellow, style violet, bifid 2/3 its length, the lower 1/3 glandular and puberulent; capsule oval, 3 mm long and broad, glandular and puberulent; mature seeds ovate, 2.7-2.9 mm long, 1.5-1.6 mm wide, dark brown, pitted, ventral surface corrugated on one side of the ridge, both margins and partly to completely across the excavations (Fig. 40). Collections: 34 (7); representative: E. Wooton s.n. (US); D. Atwood 2554, 2560, 2570, 2565, 2572, 2557, 2170, (BRY); L. Higgins 3118, 3114 (BRY, WTS); H. Bobisud 149 (NM).

HABITAT.— Sandy to gravelly or clay soils of foothills and higher mesas from 3,750 to 5,000 feet. Often associated with *Larrea* and *Prosopis*. March to May.

DISTRIBUTION.— Central New Mexico, southward to western Texas and northern Mexico (Map 16).

This taxon is related to *P. corrugata* but is distinguished from it by the smaller, darker, and more distinctly corrugated seeds, smaller, lighter corolla, and shortly exserted stamens. It has been confused to some degree with *P. bombycina* W. & S. but is easily separated from it by seed, pubescence, and vegetative features.

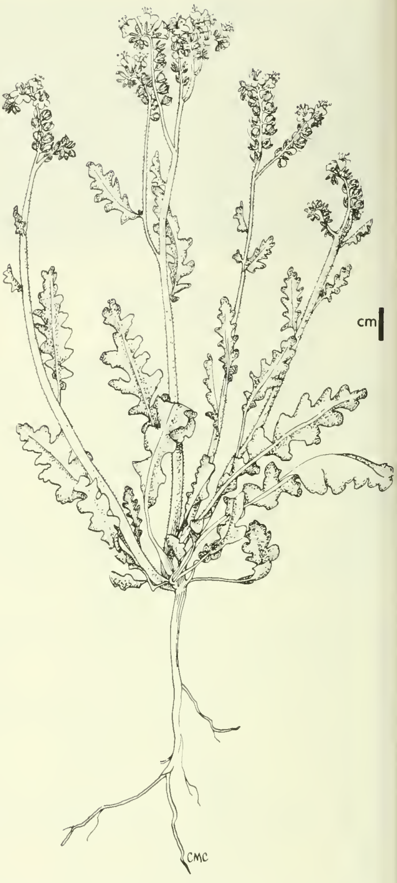


Fig. 39. *Phacelia intermedia* Wooton. D. Atwood 2560 (BRY).

21. *Phacelia mammillarensis* Atwood

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Fig. 41

Holotype: Utah: Kane Co.: Tropic Shale formation ca. 6 mi east of Glen Canyon City, along road to Warm Creek, S. Welsh and D. Atwood 9809, (BRY); Isotypes (ARIZ, ASU, BRY, GH, RM, UC, UT, UTC).

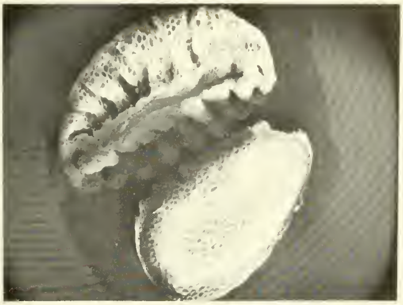
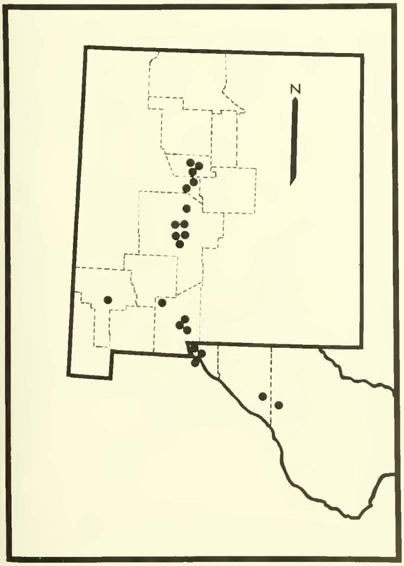


Fig. 40. Dorsal and ventral view of the seeds of *P. intermedia* Wooton. D. Atwood 2557 (BRY).

Plants annual, 0.9-5 dm tall; stems erect or sometimes branched below, yellowish or green, densely stipitate-glandular; leaves simple, oblong to lanceolate, irregularly crenate to dentate, 1-7 cm long, 0.5-3 cm wide, stipitate-glandular, setose to strigulous, with sessile leaves or nearly so; inflorescence of terminal or lateral compound scorpioid cymes, stipitate-with glandular, puberulent, hirsute to setose; sepals elliptic to oblanceolate, 4-6 mm long, 1-2 mm wide, stipitate-glandular, and hirsute to setose; corolla tubular to funnelform, the lobes pale blue to white, 5-8 mm long; stamens and style exserted 5-10 mm, the anthers lavender, the style bifid ca. 1/2 its length, the lower 1/4 pubescent; capsule subglobose, 4-5 mm long, pubescent; seeds 4, 3 mm long, 1.5 mm wide, brown, pitted dorsally, ventral surface pitted, excavated, and divided by a prominent ridge, one side of



Map 16. New Mexico and western Texas. Distribution of *P. intermedia* Wooton.

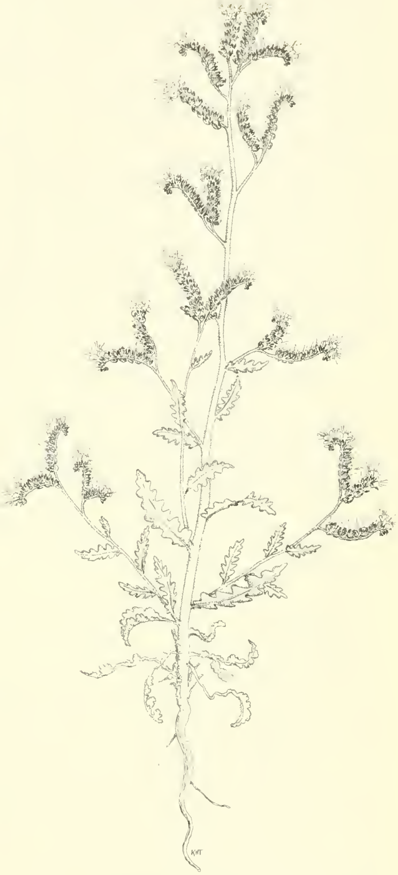


Fig. 41. *Phacelia mammillarensis* Atwood. Atwood 2632 (BRY).

the ridge corrugated, margins corrugated. Collections: 20 (15); representative: D. Atwood 2628, 2632, 1874, 1878, 4553, 3743, 3835 (BRY); B. Olsen 34 (BRY).

HABITAT.— Endemic to the Tropic Shale-Kaiparowits formations.

DISTRIBUTION.— Kane and Garfield cos., Utah, May-June.

Phacelia mammillarensis is related to *P. corrugata* Nelson but differs in its larger stature, sessile leaves (at least above), light blue to whitish corolla, and larger, more densely stipitate-glandular pubescence. The leaves are not deeply lobed or pinnate as is typical in many plants of *P. corrugata.*

22. *Phacelia neomexicana* Thurber ex Torr.

Phacelia neomexicana Thurber ex Torr. Bot. Mex. Bound. Surv. 143. 1859. Holotype: New Mexico: Grant Co.: pine woods Santa Rita Copper Mines, August 1851, Thurber 1111 (NY!); duplicate (GH). Paratype: New Mexico: 1851, C. Wright 1577 (NY, US).

Phacelia glandulosa Nutt. var. *neomexicana* (Thurber ex Torr.) Gray. Proc. Amer. Acad. 10:319. 1875.

Phacelia neomexicana Thurber ex Torr. var. *eu-neomexicana* Brand, Das Pflenzenreich IV. 251:83. 1913.

Plants annual, 0.8-6.8 dm tall; stems erect to sparsely branched, setose and with small stipitate-glandular hairs, often reddish, leafy; leaves pinnate, the secondary pinnae irregularly incised, 3-8.5 cm long, 1-4.5 cm wide, strigose and stipitate-glandular, petiolate, the petiole 1.5 cm long or less; inflorescence terminal on the main stem and lateral branches (sometimes arising from the axils of the uppermost leaves), more glandular than the stem, the individual inflorescence branches with 1-3 cymes, the cymes up to 1 dm long in fruit, flowers congested and short pedicellate (0.5 mm long); sepals linear to narrowly oblanceolate, 2.7 mm long in flower to 4.5 mm long in fruit, setose and heavily glandular; corolla campanulate, blue, ca. 4 mm long, ca. 3-3.5 mm wide, the lobes pubescent and erose; stamens exserted 1 mm, 4.5 mm long bifid 3/4 its length, glandular on the lower 1/4; capsule oval to elliptic, 4.5-4.7 mm long, 3 mm wide, setose and heavily glandular, the raphe oblanceolate; mature seeds 4, oblong, brown (immature seeds mottled with dark areas), 3.2-3.3 mm long, 1.1-1.5 mm wide, alveolate, ventral surface excavated on both sides of the ridge, alveolate. Collections: 20 (0); representative: H. Ripley and R. Barneby 5096 (RSA); W. Chapman s.n. (US); E. Greene s.n. (NY); O. Metcalfe 1506 (CAS, GH, NY); E. Wooton s.n. (US): E. Castettes 4852 (US); B. Dunn 6208 (NY).

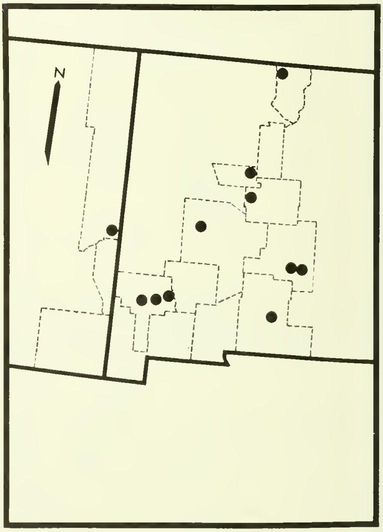
HABITAT.— Pine and oak woods in canyons and on mountain slopes, in rocky to sandy soils, from 6,800 to 9,000 feet, late July to mid-October.

DISTRIBUTION.— Apache Co., Arizona, eastward to New Mexico in Grand, Otero, Socorro, Lincoln, Torrance, Bernarillo, and Taos cos. (Map 17).

P. neomexicana is apparently most closely related to *P. denticulata* but differs from that species in its exserted stamens and style, smaller and more deeply excavated seeds. The style is also longer (4.5 mm) and the corolla is campanulate.

23. *Phacelia pallida* Johnston

Phacelia pallida Johnston. Journ. Arnold Arb. 24:98. 1943. Holotype: Mexico: Coahuila: gypsum beds on the escarpment of Canada

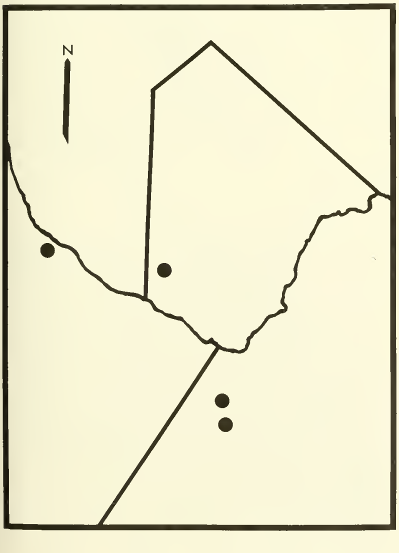


Map 17. Colorado and eastern Arizona. Distribution of *P. neomexicana* Thurber ex Torr.

Oscuro near Tanque La Luz, 26 August 1941, I. Johnston 8486 (GH!); Isotypes (GH).

Phacelia petiolata Johnston. Journ. Arnold Arb. 24:98. 1943. Holotype: Mexico: Chihuahua: 12 miles south of Ojinaga, 10-12 August 1941, I. Johnston 8040 (GH). Paratypes: Mexico: Chihuahua: 11.5 mi south of Ojinaga, 10-12 August 1941, I. Johnston 8036 (GH); Coahuila: San Lorenzo de la Laguna, 75 mi northwest of Parras, May 1880, E. Palmer 851 (GH).

Perennial plants, 1.3-3.5 dm tall; stems branched, especially at the base, erect to decumbent, puberulent, hirsute to setose with flattened multicellular stipitate glands; leaves simple, some of the lower with several small lobes borne on the petiole below the oblong, lanceolate to broadly elliptic blade, 1-7 cm long, 1-3 mm wide, long petiolate below to short petiolate above, strigose, glandular and setose, the margins irregularly crenate to sinuate; inflorescence terminal, racemose, puberulent to hispid (when old) and stipitate-glandular, cymes densely flowered, up to 15 cm long in fruit, pedicels 0.5-1 mm long; sepals oblanceolate to spatulate, 4-5 mm long, 1.4-1.7 mm wide, glandular, hirsute; corolla tubular to salverform, pale lilac, lavender, or white, 4.6 mm long, ca 4 mm wide; stamens and style exserted 5-7 mm, style bifid 3/4 its length, the lower 1/2 pubescent; capsule subglobose, 3-3.5 mm long, 2.4-2.6 mm wide, puberulent; mature seeds oblong to elliptic, brown to blackish, pitted, 2.6-3 mm long, 1-1.5 mm wide, the ventral surface excavated on both sides of the corrugated ridge, margins corrugated, dorsal surface transversely ridged. Collections: 6 (0); representative: C. Purpus 5084 (UC); O. Sperry 1694 (US); I. Johnston 8040, 8036 (GH).



Map. 18. Brewster County, Texas, Coahuila and Chihuahua, Mexico. Distribution of *P. pallida* Johnston.

HABITAT.— Apparently *P. pallida* is confined to gypsum and limestone soil.

DISTRIBUTION.— Brewster Co., Texas, southward into Coahuila and Chihuahua, Mexico (Map 18).

P. pallida and *P. petiolata* are known only from the type collections and appear to be the same entity. Therefore the author has placed *P. petiolata* as a synonym of the former. Additional collections are needed.

24. *Phacelia palmeri* Torr. ex Wats.
Fig. 42

Phacelia palmeri Torr. ex Wats. Bot. King Exped. 251. 1871. Holotype: Utah: Washington Co.: southern Utah near St. George on the Rio Virgin, 1870, Palmer 4 (NY!); Isotypes (GH, US).

Phacelia foetida Goodding. Bot. Gaz. 37:58. 1904. Holotype: Utah: Washington Co.: volcanic slopes, Diamond Valley, 16 May 1902, L. N. Goodding 833 (RM!).

Phacelia palmeri Torr. ex Wats. var. *foetida* (Goodding) Brand. Das Pflanzenreich IV, 251:79. 1913.

Phacelia palmeri Torr. ex Wats. var. *typica* Voss. Bull. Torr. Bot. Club 64:90. 1937.

Phacelia integrifolia Torr. var. *palmeri* (Torr. ex Wats.) Gray. Proc. Amer. Acad. 10:318. 1875.

Robust biennial, 2.9 dm tall; stems stout, usually solitary (sometimes with few to several branches at the base), densely glandular, hirsute and pilose, becoming hispid with age; leaves oblong to lanceolate, irregularly sinuate, crenate, dentate, or serrate, 2-13 cm long, 0.5-3 cm wide, lower densely tufted, petiolate and larger than the sessile, gradually reduced cauline leaves, stipitate-glandular and strigose; inflorescence a dense spicate thyrsus, 0.4-4.2 dm long, individual scorpioid cymes up to 14 cm long in fruit, pedicels

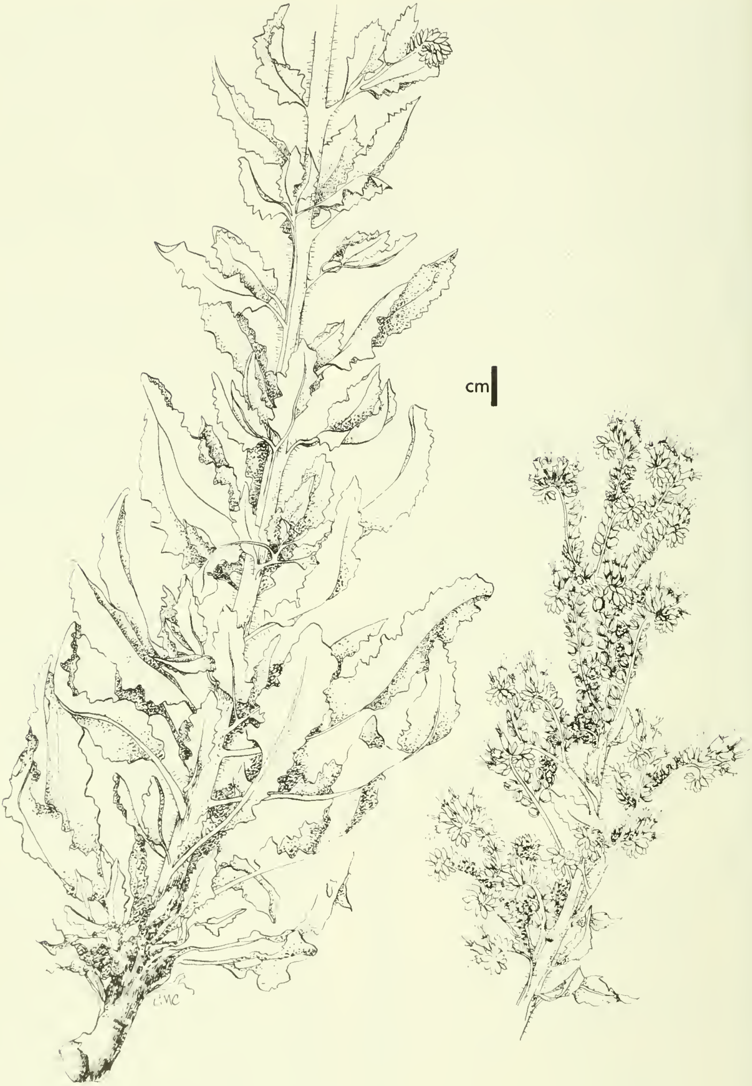


Fig. 42. *Phacelia palmeri* Torr. ex Wats. D. Atwood 1690 (BRY).

about 1 mm long in fruit; sepals oblong to spatulate, 4-5 mm long, 1-1.8 mm wide, glandular to hirsute; corolla pale (whitish, lavender, or violet), tubular, 5-7 mm long, pubescent; stamens and style exserted 5-7 mm, style bifid, the unbranched portion pubescent; capsule globose, 3.2 mm long, glandular to hirsute;

mature seeds 4, elliptic, black, 2.5 mm long, 1.5 mm wide, excavated on both sides of the ridge, the ridge corrugated on one side, pitted, margins corrugated, furrows or grooves partly corrugated, dorsal surface longitudinally pitted and transversely ridged (Fig. 43). Collections: 54 (16); representative: D. Atwood 1530, 1390, 1720, 1409 (BRY); L. Higgins 817, 1244 (BRY); D. Atwood and L. Higgins 1682 (BRY, US); D. Atwood 1723, 1712 (BRY, CAS, GH, NY, RM, US).

HABITAT.— Mostly on barren to sparsely vegetated gypsum flats, washes, and hillsides but not uncommon on rocky to sandy soil. In Diamond Valley (north of St. George) it grows on volcanic cinder cones, at 2,700 to 5,000 feet elevation, late March to August. Commonly associated with *Larrea, Juniperus, Cowania, Fallugia,* and *Atriplex.*

DISTRIBUTION.— Clark Co., Nevada, eastward to Washington and Iron cos., Utah, and Mohave Co., Arizona (Map 19).

P. palmeri is related to *P. constancei* Atwood but differs in having taller stems, larger and less revolute leaves, and coarser and longer hair. The lateral branches are fewer and less leafy, and the stems lack the reddish color characteristic of the latter. Both species occur on the Moenkopi formation but have different ranges. A form from Lake Mead, Arizona (E. U. Clover 6470 & 6230), has seeds that are not corrugated and are smaller and narrower (2.0 mm long and 1.2 mm wide), dark dorsally but brown ventrally with darker glands. However, in the material from Glendale, Nevada, the seeds are dark dorsally and lighter ventrally and are less corrugated than in typical material.

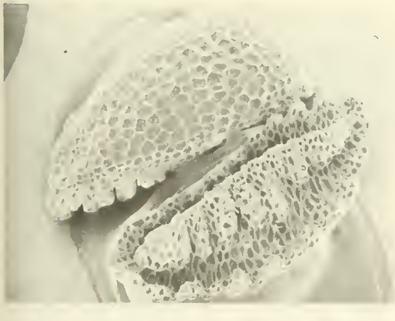
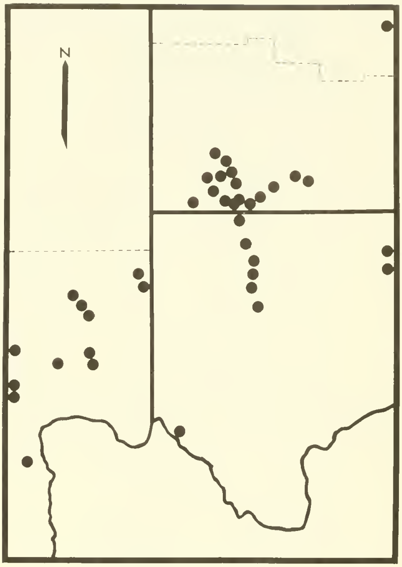


Fig. 43. Dorsal and ventral view of the seeds of *P. palmeri* Torr. ex Wats. D. Atwood 1723 (BRY).



Map 19. Southwestern Utah, northwestern Arizona, and southeastern Nevada. Distribution of *P. palmeri* Torr. ex Wats.

25. *Phacelia pedicellata* Gray

Fig. 44

Phacelia pedicellata Gray. Syn. Fl II. 1:160. 1878. Holotype: Mexico: Baja California: Lower California, 1875, Dr. Streets s.n. (GH!); Isotype (US).

Plants annual, 1-6 dm tall; stems branching or sometimes simple, brittle, villous to setose with multicellular stalked glands; leaves suborbicular to oblong, pinnately compound with 3-9 pinnae, 0.3-1.3 cm long, 1.5-11.5 cm wide, villous to setose and glandular; inflorescence of compound cymes, somewhat dichotomously branched; pedicels filiform, 2.6 mm long, densely setose to hirsute; sepals linear to oblanceolate, 2.8-7.9 mm long, 0.6-2 mm wide, setose to hirsute and glandular; corolla lobes lavender, violet, or white, the tube white, ca. 5 mm long and broad; stamens and style exserted, style pubescent, upper

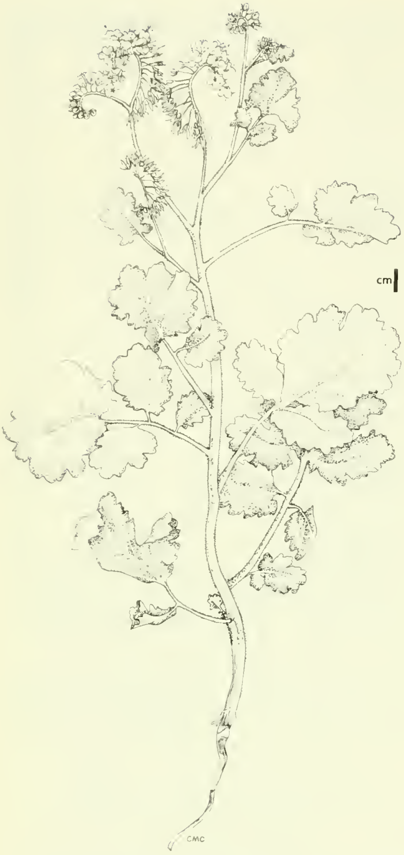


Fig. 44. *Phacelia pedicellata* Gray. W. Jepson 12482 (cas).

1/3 bifid; capsule globular, 3-3.4 mm long, 2.3-2.5 mm wide, pilose to glandular; mature seeds 4, elliptical, 3 mm long, 1.1-1.8 mm wide, ventral surface excavated, pitted to tuberculate, the ridge corrugated on one side, dorsal surface tuberculate and pitted, margins corrugated (Fig. 45). Collections: 155 (3); representative: A. Eastwood 17400 (cas, ny, us); M. Jones s.n. (pom, utc); W. Cottam 13125 (ut); T. Brandegee s.n. (ny); H. Ripley and R. Barneby 2952 (rsa); J. Howell 3952 (utc); D. Atwood 2339 (bry); S. Welsh, D. Atwood and E. Matthews 9633 (bry).

Habitat.— Dry gravel and sandy washes, often in the shade of large boulders, limestone cliffs, and as understory of larger plants, below sea level in Death Valley to 5,000 feet elevation. It has been collected in the middle of February in Mexico but usually flowers from March to the middle of June.

Distribution.— Southern Nevada in Nye and Clark cos., southward through San Bernardino to central Baja California, eastward to Coconino, Graham, Gila, Pinal, and Pima cos., Arizona (Map 20).

Phacelia pedicellata is most closely related to *P. scariosa* but differs in having narrower, longer, and more pubescent calyx lobes, a more compound and congested inflorescence, and a heavier, glandular, villous, and setose pubescence. The leaves have 3-9 pinnae, whereas those of *P. scariosa* have only 3-5 lobes, and the style is more pubescent. That they are related is indicated by the similar seeds, corolla, pedicels, and brittle stems.

26. *Phacelia popei* Torr. & Gray
Fig. 46

Phacelia popei Torr. & Gray. Pacific Rail. Rep. Explor. Mississippi 2:172. 1885. Holotype: Texas: Llano Estacado, no date, Captain Pope s.n. (gh!). Paratype: Texas: Pecos Co.: C. Wright 1578 (gh, ny, us).

Phacelia popei Torr. & Gray var. *typica* Voss. Bull. Torr. Bot. Club 64:94. 1937.

Phacelia similis Wooton & Standley. Bull. Torr. Bot. Club 36:111. 1909. Holotype: New Mexico: Sierra Co.: on the plains near Nutt Station, 12 May 1905, O. Metcalfe 1665 (ny!).

Phacelia popei Torr. & Gray var. *similis*

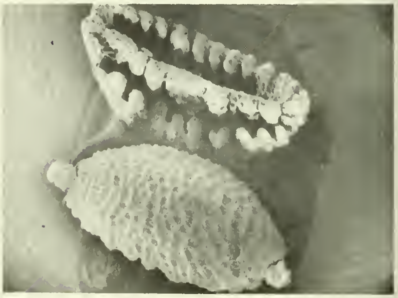
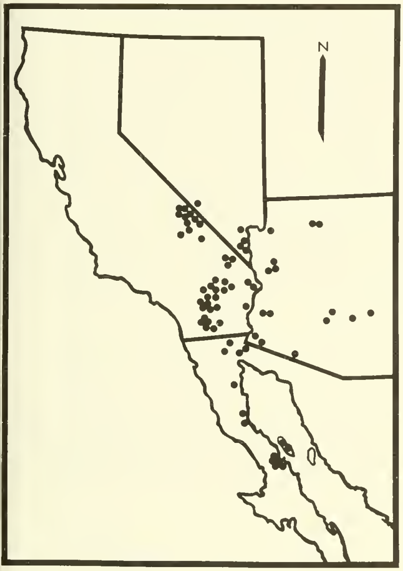


Fig. 45. Dorsal and ventral view of the seeds of *P. pedicellata* Gray. M. Beal (jeps).



Map 20. Part of southwestern United States and adjacent Baja California, Mexico. Distribution of *P. pedicellata* Gray.

(Wooton & Standley) Voss. Bull. Torr. Bot. Club 64:94. 1913.

Phacelia glandulosa A. Gray in Brand, Das Pflanzenreich IV, 251:84. 1913, in synonomy.

Phacelia depauperata Wooton & Standley. Contr. U. S. Natl. Herb. 16:163. 1913. Holotype: New Mexico: Caves Co.: Arroyo Ranch near Roswell, 1903, D. Griffiths 4249 (US!).

branched from the base, 0.5-3.6 dm tall, with simple spreading or bent hirsute and somewhat glandular hairs intermixed with a finer pubescence; leaves narrowly oblong, pinnate to bipinnate, with linear or lanceolate divisions, 2-15 cm long, 1-3 cm wide, petiolate, strigose to glandular, except on the petioles and then like that on the stems; inflorescence of compound scorpioid cymes, the cymes crowded, terminal, up to 10 cm long in fruit, glandular and hirsute, flowers nearly sessile (pedicels ca. 0.5 mm long); corolla campanulate, blue to purplish, 3.5-7 mm long and broad, pubescent; sepals oblanceolate to spatulate, somewhat keeled (at least at the base), 2.3-3.9 mm long, 1-1.8 mm wide, glandular, hirsute; stamens and style exserted, style exserted ca 2 mm longer than the stamens, bifid 2/3 its length, lower 1/3 pubescent; capsule globose, 2.3-2.5 mm long, 2.4-3.1 mm wide, glandular and pilose; mature seeds 4, cymbiform, ovate, brown, 1.8 mm long, 1.4 mm wide, favose to reticulate, ventral surface deeply excavated on both sides of the ridge, dorsal surface reticulate and transversely ridged (Fig. 47). Collections: 150 (11); representative: D. Atwood 2096a, 2095, 2268, 2266, 2153, 2159, 2131, 2133, 2134 (BRY); L. Higgins 3083, 3025 (BRY, WTS); R. Barneby 12593 (CAS, NY); M. Jones 25750 (POM); A. Hershey s.n. (CAS).

HABITAT.— Commonly in sandy or sandy clay soil of roadsides. Less commonly in limestone or rocky soil and associated with *Larrea*, *Prosopis*, *Yucca*, or short grass prairie. Mid-February to late May.

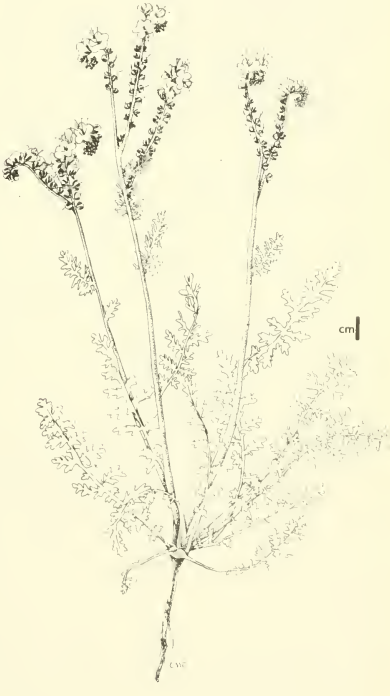


Fig. 46. *Phacelia popei* Torrey & Gray. L. Higgins 2931 (BRY).

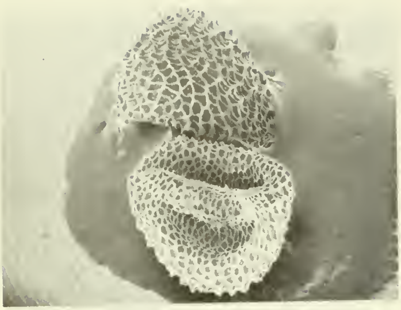
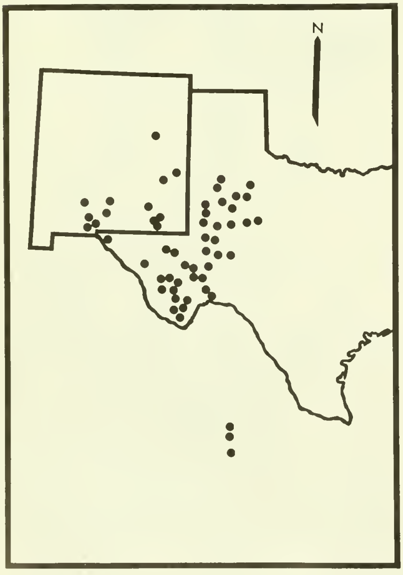


Fig. 47. Dorsal and ventral view of the seeds of *P.popei* Torrey & Gray. V. Cory 13616 (GH).

Distribution.— West central Texas from Dickens and Lubbock cos. southward to southwestern Texas, westward to New Mexico from Roosevelt Co., westward to Sierra and Luna cos., Nuevo León, Mexico (Map 21).

Wooton and Standley (1909), in their original description, indicated that *P. similis* was most closely related to *P. arizonica* but failed to mention *P. popei*. Comparison of the type material of the two entities leaves little doubt that they are identical. Also, *P. arizonica* is very distinct from *P. popei*. Torrey and Gray (1885), in their original description of *P. popei*, indicated that the corolla was "apparently white." I have seen this taxon in the field in Texas and New Mexico and find that the corolla is not white or only seldom so. The flowers of some specimens turn white upon drying, and this may have been the case with the type material.



Map 21. New Mexico, Texas, and Nuevo León, Mexico. Distribution of *P. popei* Torrey & Gray.

27. *Phacelia rafaelensis* Atwood
Fig. 48

Phacelia rafaelensis Atwood. Rhodora 74(800): 454-457. 1972. Holotype: Utah: Wayne Co.: Capitol Reef National Monument, 12 June 1969, D. Atwood and L. Higgins 1834 (BRY!).

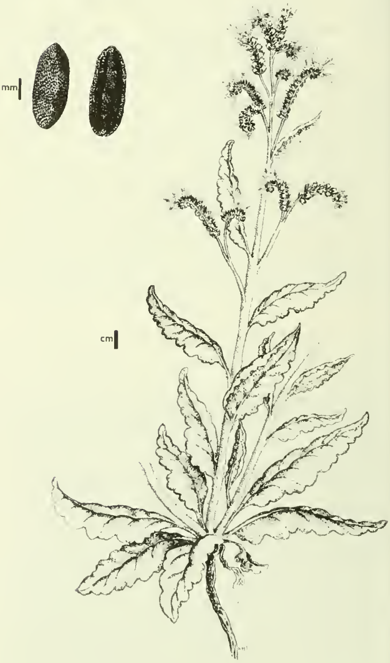


Fig. 48. *Phacelia rafaelensis* Atwood. D. Atwood and L. Higgins 1834 (BRY).

Erect biennial herb, 0.8-5.4 dm tall; stems stout, simple or sometimes branched at the base, olive green to brownish glandular, and hirsute; basal leaves petiolate, dentate, crenate to pinnatifid, 2-7 cm long; 0.5-1.5 cm wide, strigose to hirsute, cauline leaves sessile, undulate to crenate or dentate, oblong-lanceolate, 1-10 cm long, 0.5-3.5 cm wide, strigose to hirsute and sparsely stipitate-glandular; inflorescence mainly terminal, paniculate, some axillary, flowers nearly sessile; sepals oblanceolate to spatulate, 3-4 mm long in flower, 5-6 mm long in fruit, 1-1.7 mm wide, glandular and hirsute; corolla tubular, pale and grooved with the lobes somewhat spreading, 5-6 mm long; stamens and style exserted only 3-5 mm, anthers dull in color, style bifid 3/4 its length, the lower half pubescent; capsule globose, 4-5 mm long, stipitate-glandular and hirsute; mature seeds 4, elliptic to oblong, 3.5-4 mm long, 1.5-2 mm wide, ventral surface alveolate, lighter than the dorsal surface, excavated and divided by a prominent ridge, the ridge sometimes corrugated along one side, the margins usually entire, dorsal surface brown and less deeply pitted, the surface often smoothish (Fig. 49). Collections: 33 (19); representative: M. Jones s.n. (POM); H. Ripley and R. Barneby 4362 (RSA); W. Cottam 13313 (UT); D. Atwood 1530, 1853, 1843, 1855, 1847, 1703, 1417, 1698, 1860 (BRY); S. Welsh, D. Atwood, and G. Moore 9846, 9844, 9903 (BRY); D. Atwood 1390 (BRY).

Habitat.— Clay hills of the Moenkopi formation, May to June.

Distribution.— Emery Co., Utah, southward to Kane Co., Utah, and Mohave Co., Arizona, eastward to Washington Co., Utah (Map 22).

Phacelia rafaelensis is related to *P. utahensis* but differs in having a slightly tubular and grooved corolla, with the lobes somewhat spreading and the stamens and style exserted only 3-5 mm. The filaments and stamens are dull in color, and the ridge is sometimes corrugated.

28. *Phacelia robusta* (Macbr.) Johnst.

Fig. 50

Phacelia robusta (Macbr.) Johnst. Journ. Arnold. Arb. 24:97. 1943.

Phacelia integrifolia Torr. ex Wats. var. *robusta* Macbride. Contr. Gray Herb. 49:25. 1917. Holotype: Texas: Presidio Co.: Chinati Mountains, no date, Harvard 250 (GH!).

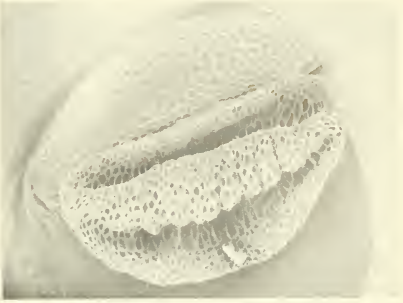
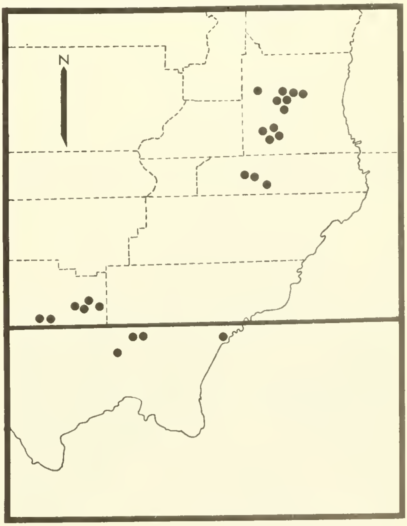


Fig. 49. Dorsal and ventral view of the seeds of *P. rafaelensis* Atwood. S. Welsh et al, 9903 (BRY).

Robust, viscid annual or biennial, 4.5-12 dm tall; stems branched at the base or simple, brownish, puberulent, pilose and densely glandular, the glandular hairs flattened, stipitate, unicellular to multicellular; leaves broadly ovate to orbicular, irregularly crenate to sinuate, sometimes with a single lobe below the leaf blade, 2-11.5 cm long, 1.5-9 cm wide, gradually



Map 22. Southern Utah and northwestern Arizona. Distribution of *P. rafaelensis* Atwood.

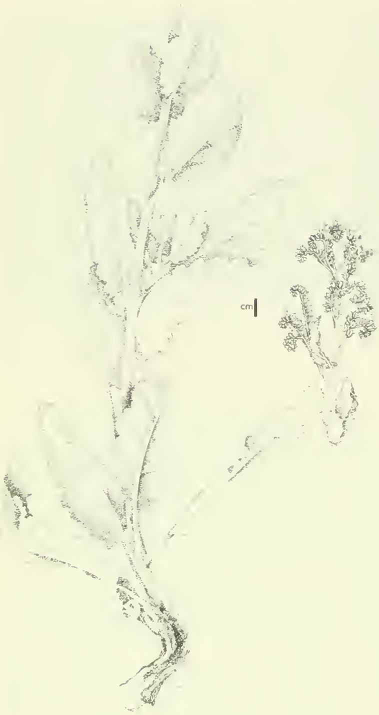


Fig. 50. *Phacelia robusta* (Macbride) Johnston. I. Higgins 3268 (BRY).

reduced upwards, puberulent, stipitate-glandular, setose to hirsute, the lower long-petiolate to subsessile above; inflorescence of compound scorpioid cymes, the cymes up to 1.3 dm long in fruit, pubescence the same as that of the stem, pedicels 1-1.7 mm long; sepals spatulate, 4.5-5.8 mm long, 1.5-2.5 mm wide; corolla salverform, pale lavender, 5-6 mm long, ca. 4 mm wide, pubescent; stamens and style exserted 4-6 mm, style bifid 3/4 its length, lower 1/2 pubescent; capsule subglobose, 3.9-4.1 mm long, 2.8-3mm wide, puberulent to strigose; mature seeds oblong to ovate, reddish brown, 2.9-3.7 mm long, 1.1-1.7 mm wide, ventral surface excavated on both sides of the corrugated ridge, pitted, the margins at least partly corrugated (Fig. 51). Collections: 36 (0); representative: C. Pringle 255 (UC, RSA); E. Palmer 34077 (NY); L. Hinckley 829 (GH, NY); U. Waterfall 7316, 8255, 8283 (UC); C. Smith 289 (UC); G. Stevens 1636 (GH, NY); L. Higgins 3256, 3182 (BRY, WTS).

Habitat.— Gravelly sand bars, clay slopes, and rocky hills from ca. 3,500 to 6,000 feet elevation, March to August.

Distribution.— Barber Co., Kansas, southward through Woods, Blaine, Custer, Washita, and Horman cos., Oklahoma, to north central and southwestern Texas and Chihuahua, Mexico (Map 23).

This taxon has been confused with *P. intergrifolia*, but it is easily recognized by the white, tubular corollas, robust habit, and larger, less glandular leaves. In seed characters, *P. robusta* is similar to *P. integrifolia* var. *texana*. There appear to be several distinct entities included within this taxon. The material in north central Texas is disjunct in distribution from that in Presidio and Brewster cos., but additional material is needed to determine if there are sufficient morphological characters to delineate the populations. Also, specimens from southern Colorado and adjacent New Mexico appear to be different and need to be investigated further.

29. *Phacelia rupestris* Greene

Phacelia rupestris Greene, Leaflets 1:152. 1905. Holotype: New Mexico: Sierra Co.: south end of the Black Range, 1 mi west of Hillsboro, 25 June 1904, O. Metcalfe 1012 (GH!); Isotypes (CAS, NY, POM, UC, UC, US, US, US).

Phacelia congesta Hook. var. *rupestris* (Greene) Macbride. Contr. Gray Herb. 49:25. 1917.

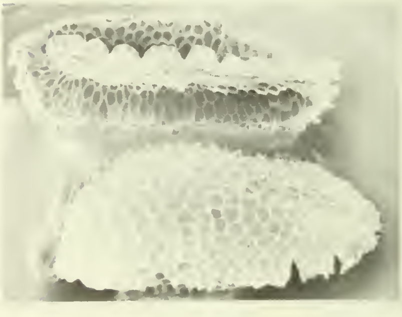
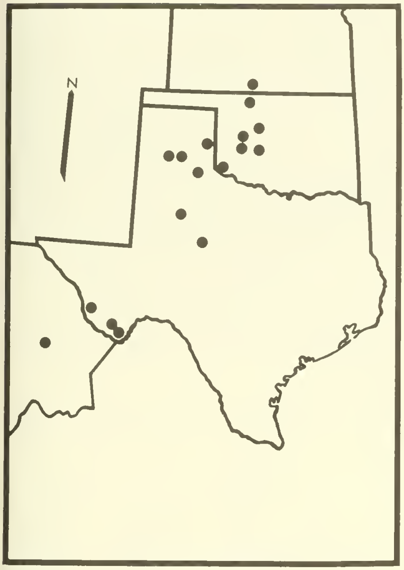


Fig. 51. Dorsal and ventral view of the seeds of *P. robusta* (Macbride) Johnston. L. Hinckley 829 (NY).



Map 23. Southern Kansas, Texas, and adjoining states. Distribution of *P. robusta* (Macbride) Johnston.

Perennial plants (sometimes flowering the first year), 1-6 dm tall; stems 1-many, usually from a woody caudex, pubescence of whitish hairs, these hispid to setose and finer, sometimes glandular (these not multicellular glands); leaves pinnately compound, the terminal part incompletely 3-5 lobed and larger than the lower pinnae, 1.5-10 cm long, 1-5 cm wide, setose to densely pilose; inflorescence of terminal compound scorpioid cymes, individual cymes 1.5-4.5 cm long, pedicels 1.5-2.5 mm long; sepals linear to oblanceolate, 3-4.8 mm long, 0.5-0.8 mm wide, setose to hirsute; corolla campanulate, white, 2-4 mm long and broad, lobes pubescent; stamens and style exserted up to ca. 2 mm, anthers dull blue; style 5-6 mm long, bifid over 1/2 its length, the lower unbranched portion pubescent; capsule oval to ovate, 2.6-3 mm long, 2.4-2.5 mm wide, finely pubescent with a few long hairs near the apex; mature seeds 4, brown, 2.1-2.7 mm long, 1-1.1 mm wide, elliptical to oblong, reticulate scabrous, ventral surface excavated on both sides of the ridge (Fig. 52). Collections: 78 (1); representative: L. Goodding 2330 (GH, RM, UC); H. Rusby s.n. (CAS, US); B. Maguire 11204 (BRY); A. Nelson 1248 (NY); C. Pringle 162 (MEXU, NY, US); E. Wooton s.n. (NY); D. Dunn 8525 (UC).

HABITAT.— Growing on coarse, sandy soil and gravel bars, moist shady crevices of limestone cliffs, and ledges in canyons and arroyos, at 2,100 to 6,500 feet elevation. Flowering commonly occurs from late June to late August but sometimes as early as mid-March and as late as the last of October. Usually associated with *Larrea*, *Acacia*, *Lippia*, *Fallugia*, *Chilopsis*, and *Opuntia* at lower elevations and with *Quercus*, *Cercocarpus*, *Juniperus*, *Pinus*, and *Fraxinus* at higher elevations.

DISTRIBUTION.— Southern New Mexico from Socorro Co. westward to Pinal, Pima, and Cochise cos., Arizona, and southward to southwestern Texas and adjacent Mexico (Map 24).

This entity is closely related to *P. congesta* but differs in having smaller, white corollas, shorter and fewer flowered cymes, a perennial habit, and the abscence of multicellular glands. At times it apparently flowers in the first year, at least in the more southern parts of its range.

30. *Phacelia scariosa* T. S. Brandegee

Fig. 53

Phacelia scariosa T. S. Brandegee. Proc. Calif. Acad. Sci. 2:185. 1889. Holotype: Mexico: Baja California: Lower California, 12 January 1889, Brandegee s.n. (UC!); duplicates (NY, US).

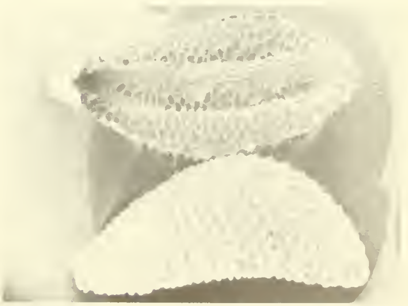
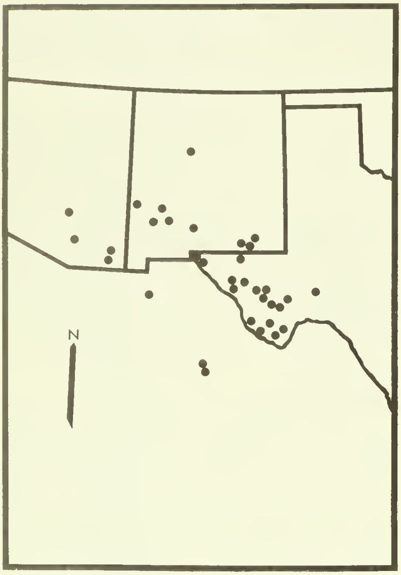


Fig. 52. Dorsal and ventral view of the seeds of *P. rupestris* Greene. W. Eggleston 16341 (US).



Map 24. Southeastern Arizona, New Mexico, southwestern Texas, and adjoining Mexico. Distribution of *P. rupestris* Greene.

Plants annual, 0.5-4 dm tall; stems branching from the base (sometimes dichotomously), finely glandular and pilose; leaves ovate to oblong, deeply cleft to more often pinnately divided with 3-5 pinnae, terminal leaflet usually trilobed and larger than the other leaflets, 1.5-8 cm long, 1-5.5 cm wide, strigose and somewhat glandular; inflorescence paniculate to racemose, glandular to villous, cymes elongate, open, up to 11 cm long, pedicels filiform, 3 mm long in flower, up to 8 mm long in fruit; corolla broadly campanulate, bluish to lavender, with white throat and tube, 4 mm long, 4-5 mm wide, pubescent; sepals obovate, 2-3 mm long in flower, becoming broadly obovate and conspicuously enlarged and scarious in fruit, 4.5-7.6 mm long, 2.3-3.7 mm wide, glandular to villous; stamens and style exserted 1-2 mm, style cleft 1/3 its length, lower 1/3 pubescent; capsule globular, 3.3-3.7 mm long, 2.6-3.5 mm wide, glandular to pilose; mature seeds 4, brown, elliptical, 2.5-3 mm long, 1.2-1.3 mm wide, ventral surface divided by a prominent ridge, pitted, margins corrugated, the ridge corrugated on one side, dorsal surface curved, pitted (Fig. 54). Collections: 42 (0); representative: C. Orcutt 13 (CAS, NY, US); M. Jones 24069 (POM, RM); T. Brandegee s.n. (UC); R. Moran 3890 (UC); D. Porter 236 (CAS, MEXU); F. Shreve 7023 (US).

HABITAT.— Sandy, gravelly washes, rocky hillsides, and lava flows from 200 to 5,000 feet elevation. Apparently a winter annual, flowering from late October to mid-June.

DISTRIBUTION.— Lower California and adjacent Sonora, Mexico (Map 25).

Phacelia scariosa is apparently related to *P. pedicellata* and is discussed under that species.

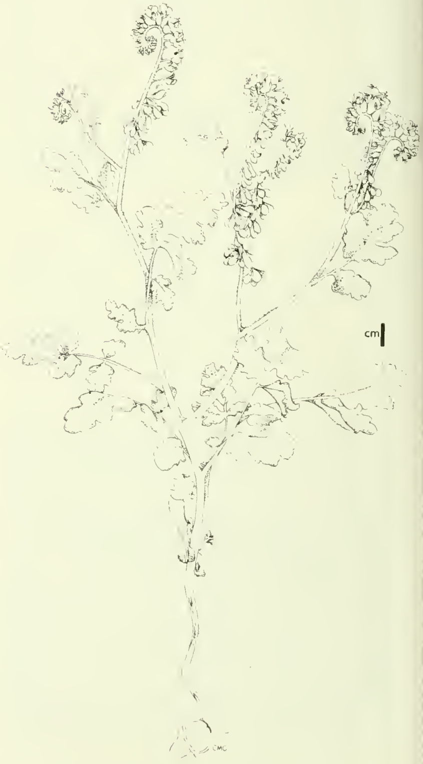


Fig. 53. *Phacelia scariosa* T. S. Brandegee. I. Wiggins 7887 (US).

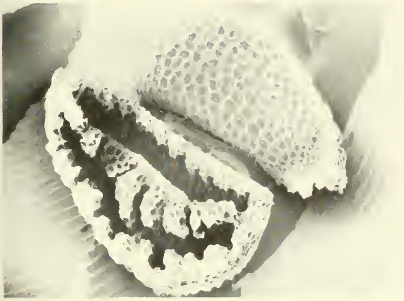
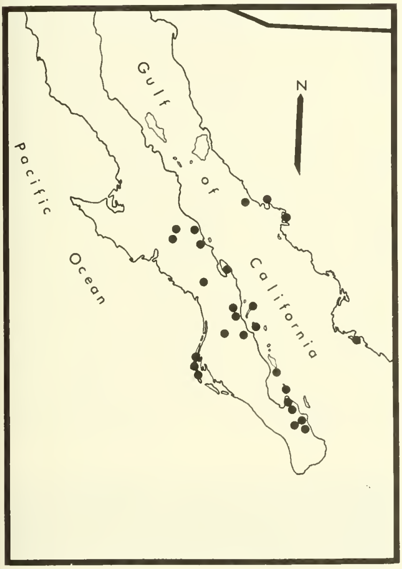


Fig. 54. Dorsal and ventral view of the seeds of *P. scariosa* Brandegee. I. Johnston 3884 (CAS).



Map 25. Baja California and Sonora, Mexico. Distribution of *P. scariosa* Brandegee.

31. *Phacelia serrata* Voss
Fig. 55

Phacelia serrata Voss. Bull. Torr. Bot. Club 64:88-89. 1937. Holotype: Arizona: Coconino Co.: San Francisco Mountains, May-October 1900, C. A. Purpus 8064 (POM!); Isotypes (UC, US). Paratypes: Arizona: Coconino Co.: vicinity of Flagstaff, 15 July 1898, Macdougal 288 (NY, RM, US, US); volcanic scoria, San Francisco Mountains, September 1884, Lemmon and wife (UC, UC, US); Sunset Mountain, Flagstaff, 21 August 1915, H. Rusby s.n. (NY).

Phacelia macdougalii Heller in Brand. Das Pflanzenreich IV, 251:80. 1913, as synonym.

Annual plants, 1-3.4 dm tall; stems erect, simple or branched at the base, with simple setose, hirsute and multicellular

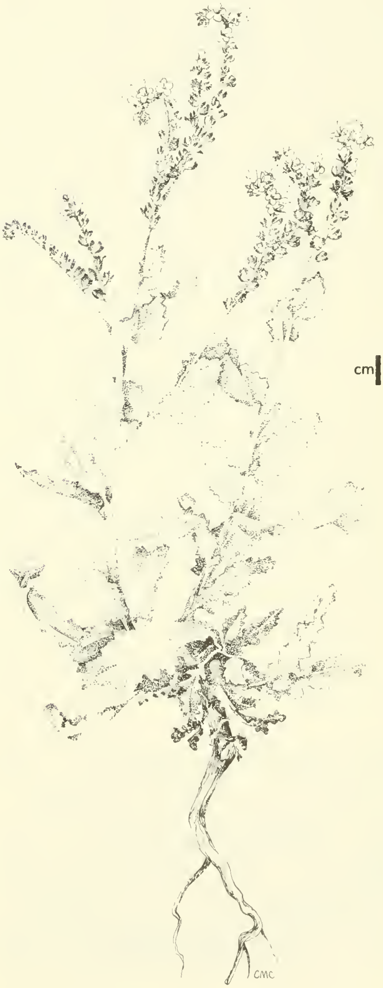


Fig. 55. *Phacelia serrata* Voss. J. T. Howell and G. True 45184 (CAS).

glandular hairs; leaves lanceolate, serrate, dentate to shallowly lobed, 1.4 cm long, 0.5-2 cm wide, with a basal leaf cluster, especially when young, gradually reduced upward, the upper sessile or nearly so, the lower with a petiole up to 1.5 cm long, setose, hirsute and glandular; inflorescence of compound scorpioid cymes, setose, puberulent with multicellular stipitate glands, pedicels up to 1 mm long; sepals elliptical to oblanceolate, more or less keeled at the base, 3.5-6.5 mm long, 1.5-2 mm wide, setose, puberulent and stipitate-glandular; corolla rotate (appearing tubular in some pressed specimens), blue to light violet, 3-4 mm long and broad, pubescent; stamens and style exserted, style bifid 3/4 its length, lower 1/4 pubescent; capsule subglobose, 2.8-3.5 mm long, 2-2.5 mm wide, glandular and puberulent; mature seeds 4, elliptical to oblong (sometimes unequally so when one of the margins is involute), dark brown, 3-3.2 mm long, 1-1.3 mm wide, excavated and divided by a prominent ridge, the ridge corrugated on one side, the margins corrugated, pitted and often one or both involute, dorsal surface smooth and shiny to somewhat dull, sometimes faintly pitted, the tip and margins darker for part of their length (or at least different in appearance from the rest of the dorsal surface). Fig. 56. Collections: 15 (2); representative: J. Hill s.n. (US); L. Goodding 1526 (UC); D. Atwood 2586 (BRY); D. Dunn 12644 (RSA); H. Hansen 615 (RM); J. Howell and G. True (BRY, CAS).

HABITAT.— Confined to volcanic scoria slopes of open yellow pine forest and juniper flats and hills. Flowering from late June to mid-September, 5,900 to 7,150 feet.

DISTRIBUTION.— In and around Sunset Crater National Monument and San Francisco Mountains north of Flagstaff, Coconino Co., Arizona.

The relationships of this entity to other taxa in this group are questionable at the present time. Part of the paratype material cited by Voss (1937) belongs to *P. palmeri*. The specimen in question is Palmer 335 (GH, NY) and was probably collected in southern Utah or the extreme northern part of Arizona in Mohave Co. The label bears the data southern Utah-northern Arizona. Brand (1913) inadvertently listed *P. macdougalii* as a synonym of *P. integrifolia* Torr. even though it was only a manuscript name and had never been published. I have seen the specimens in question and conclude that they are referable to *P. serrata* Voss. Voss (1937) described *P. serrata* but failed to mention *P. macdougalii.*

32. *Phacelia splendens* Eastwood

Fig. 57

Phacelia splendens Eastwood. Zoe 4:9. 1893. Holotype: Colorado: Mesa Co.: Grand Junction, 19 May 1892, A. Eastwood s.n. (CAS?); Isotypes (UC, UC, US, sketch at NY).

Phacelia glandulosa Nutt, subsp. *splendens* (Eastwood) Brand. Das Pflanzenreich IV, 251:83. 1913.

Plants annual, 0.5-2.7 dm tall; stems erect, simple or branched leafy, puberulent, with scattered stipitate-glandular hairs; leaves pinnatifid, 2-7.5 cm long, 0.7-4 cm wide, petiolate, leaf blade essentially glabrous (pubescent only on the petiole and rachis or lower portion of the pinnae); inflorescence terminal on each branch and the main stem, cymes compact and densely flowered, pedicels short but lengthening to as much as 1.7 mm in fruit, slightly more pubescent than the stem; sepals linear to narrowly oblanceolate, 2.5-3 mm long in flower, 4-4.4 mm long in fruit, 0.6-1 mm wide, hirsute and with a few scattered glandular hairs; corolla campanulate, the lobes bright blue, the tube yellowish, 4-8 mm long and broad, glabrous to sparsely pubescent; stamens and style exserted 7-11 mm, the filaments blue, anthers yellow, style bifid ca. 2/3

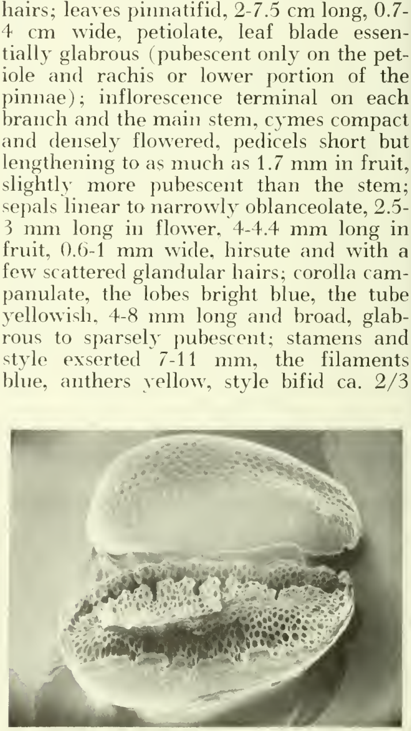


Fig. 56. Dorsal and ventral view of the seeds of *P. serrata* Voss. J. T. Howell and G. True 45184 (BRY).

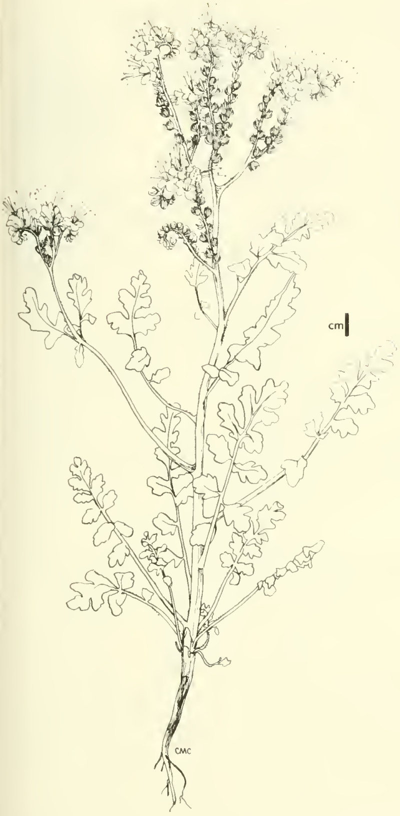


Fig. 57. *Phacelia splendens* Eastwood R. Barneby 12797 (CAS).

its length, the undivided portions puberulent and glandular; capsule subglobose, 4-4.5 mm long, 3-3.5 mm long, 1.5 mm wide, finely favose, the ventral surface excavated on both sides of the ridge, the ridge with evident corrugations on one side, the margins more or less revolute (Fig. 58). Collections: 23 (4); representative: W. Weber 7509 (CAS, RM, RSA, UC); D. Atwood 2532 (BRY); D. Atwood and L. Higgins 1814 (BRY); L. Higgins 3302 (BRY, WTS); S. Welsh 756 (BRY); R. Barneby 12743 (CAS, NY, RSA); E. Payson 671 (GH).

HABITAT.— Apparently confined to the Mancos Shale formation, 4,500 to 6,000 feet elevation. Commonly associated with *Atriplex*, but in Mesa Verde National Monument it was collected in pinyon-juniper. Mid-May to mid-July.

DISTRIBUTION.— Known only from western and southwestern Colorado and northwestern New Mexico (Map 26).

This species is related to *P. corrugata* and *P. utahensis* and may be a link between the two complexes. It can be distinguished from the former by its nearly glabrous and more-divided leaves, yellowish corolla tube, and different-textured and less-corrugated seeds. From the latter, it differs in having a shorter and less-glandular indument, a less-robust and less-branched habit, and different seeds. The seeds were reported by both Eastwood (1893) and Voss (1937) as lacking corrugations. Observations of mature seeds of *P. splendens* demonstrate that there definitely are evident corrugations on one side of the ridge and sometimes on one of the incurved margins.

33. *Phacelia utahensis* Voss

Fig. 59

Phacelia utahensis Voss. Bull. Torr. Bot. Club 64:135. 1937. Holotype: Utah Sanpete Co.: Gunnison, 7 June 1910, M. Jones s.n. (POM).

Plants stout, erect annuals, 0.8-5.8 dm tall; stems usually simple, sometimes branched at the base, brownish to yellowish, densely glandular and finely pubescent; leaves linear to narrowly lanceolate, strigose to ciliate on the margins, with scattered glands (especially the upper), 1.5-12 cm long, 0.5-1.5 cm wide, the mar-

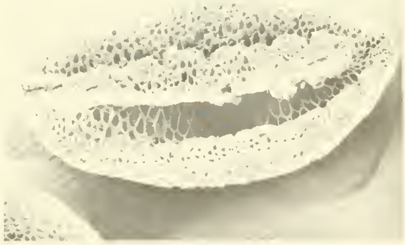
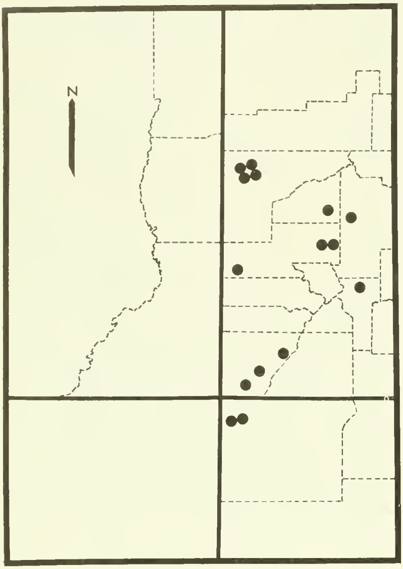


Fig. 58. Dorsal and ventral view of the seeds of *P. splendens* Eastwood. D. Atwood and L. Higgins 1814 (BRY).



Map 26. Southwestern Colorado and adjoining states. Distribution of *P. splendens* Eastwood.

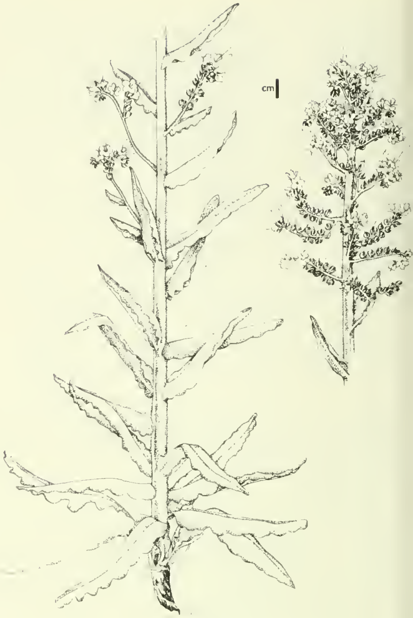


Fig. 59. *Phacelia utahensis* Voss. D. Atwood and L. Higgins 1624 (BRY).

gins often revolute, crenate, undulate to irregularly dentate, basal ones petiolate and dense, the upper sessile, auriculate to cordate; inflorescence thyrsoid, up to 3.4 dm long, often with a few lateral, leafy inflorescence branches below, stipitate-glandular and finely pubescent, cymes mostly in pairs, (or 1-3), up to 4 dm long in fruit, densely flowered, the pedicels, 1-1.5 mm long; sepals oblanceolate, 3-4 mm long, 0.8-1.1 mm wide, glandular and hirsute; corolla rotate to campanulate, the lobes bluish to violet, the tube yellowish, ca. 3-4 mm long, ca. 6 mm broad, glabrous; stamens exserted 9-10 mm, filaments violet, anthers yellow; style exserted ca. 10 mm, bifid 3/4 its length, the lower 1/4 setose and glandular; capsule globose to subglobose, 3.5-4.1 mm long, 2.6-3.5 mm wide, glandular and setose; mature seeds 4, elliptical, dark (reddish), the dorsal surface faintly pitted, the ventral surface excavated on both sides of the ridge, often lighter than the dorsal surface, pitted with the markings in the excavations longer (transversely) than those of the ridge or margins, the ridge sometimes faintly corrugated on one side. Collections: 22 (13); representative: J. Howell and G. True 44640 (BRY, CAS); L. Higgins 1624 (BRY); D. Atwood 1520, 1893, 1835, 1684, 1892, 1894, 1895, 1526, 1519, 1518, 1525, 1528, 1527 (BRY).

HABITAT.— Endemic to the Arapian Shale formation.

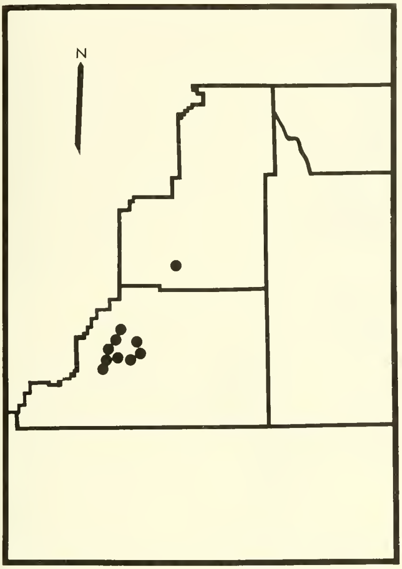
DISTRIBUTION.— Sevier and Sanpete cos., Utah, from 5,500 to 5,700 feet, April to June (Map 27).

34. *Phacelia vossii* Atwood

Fig. 60

Phacelia vossii Atwood. Rhodora 74(800):462-465. 1972. Sierra Madre Oriental, calcite and limestone hills beyond Pablillo toward Santa Clara, ca. 15 mi southwest of Galeana, 18 July 1934, C. H. Mueller 1075 (GH!); Isotype (MEXU). Paratype: Mexico: Nuevo León: Hacienda Pablillo, Galeana, 13 August 1936, M. Taylor 156 (NY, UC).

Perennial plants, 2.1-7.3 dm high; stems erect from a woody caudex, with hirsute to setose and stipitate-glandular hairs; leaves



Map 27. Central Utah in Sanpete and Sevier counties. Distribution of *P. utahensis* Voss.

linear to lanceolate, 2-11 cm long, 0.5-2.2 cm wide, revolute, ventral surface heavily glandular, dorsal surface hirsute, with scattered stipitate-glandular hairs, margins dentate to irregularly toothed, petiolate, the petiole up to 1.5 cm long; inflorescence axillary to terminal, scattered along the stems for as much as 1/2 its length or less, consisting of simple to compound scorpioid cymes, individual cymes up to 7.5 cm long in fruit, pedicels up to 2 mm long in fruit, glandular and hirsute; corolla tubular to short campanulate, pale lavender (rarely white), 5.5 mm long; sepals oblanceolate to spatulate, 4.6 mm long, 1.5-2 mm wide, glandular and hirsute; stamens exserted, filaments purple, anthers greenish blue; style exserted ca. 2 mm longer than the stamens ca. 9 mm long, bifid for 3/4 its length, lower 1/4 pubescent; capsule ovate, 3.7 mm long, 2.5-2.7 mm wide, glandular and strigose; immature seeds 4, elliptical to oblong, brown, 2.5-3.1 mm long, 1-1.4 mm wide. Collections: 4 (1); representative: known only from the type collections and D. Atwood and J. Reveal 5985, 25 September 1973 (BRY).

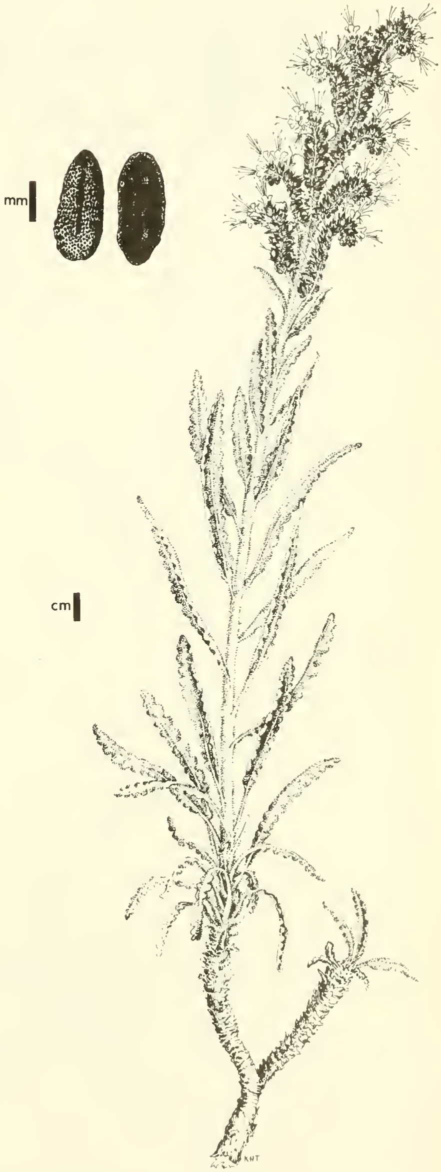


Fig. 60. *Phacelia vossii* Atwood. G. Mueller 1075 (MEXU).

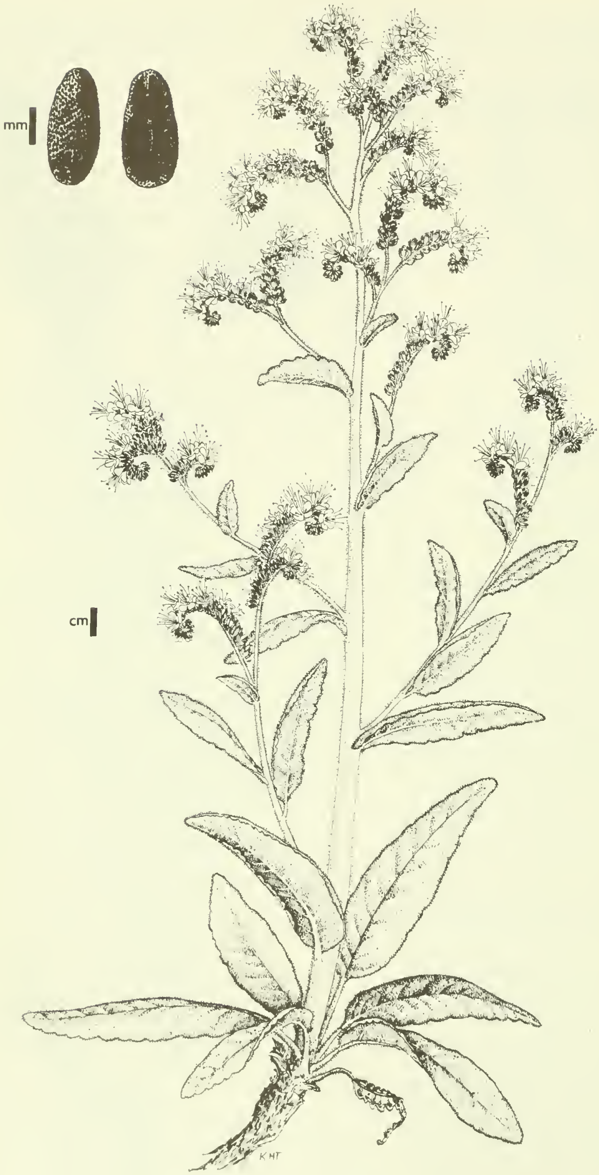


Fig. 61. *Phacelia welshii* Atwood. D. Atwood 2605 (BRY).

HABITAT.— Apparently endemic to calcite and limestone soils.

DISTRIBUTION.— Known only from the type locality near Galeana in the state of Nuevo León, Mexico.

The corollas of the type specimens have faded to white, which is a common occurrence in several species of this group.

This taxon appears to be related to *P. pinnatifida* Griseb., which, according to Brand (1913), occurs in the Andes of South America in Peru, Bolivia, and Argentina.

35. *Phacelia welshii* Atwood
Fig. 61

Phacelia welshii Atwood. Rhodora 74(800):465-468. 1972. Holotype: Arizona: Coconino Co.: along highway 89 just north of Gray Mountain, 19 May 1970, D. Atwood 2608 (BRY!); Isotypes (ARIZ, ASC, B, BRY, CAS, COLO, DIXIE, GH, NY, POM, RM, RSA, US, US, UT, UTC, WSC, WTS).

Annual, 1-5.5 dm tall; stems more or less yellowish to green, simple or branched, leafy, hirsute and densely covered with multicellular stipitate glands; leaves oblong to lanceolate, 1.5-8 cm long, 0.5-2.7 cm wide, hirsute and densely glandular, the margins often revolute, undulate and dentate, the basal leaves clustered, petiolate, the petiole 2 cm long or less, cauline leaves sessile or nearly so, often cordate at the base; inflorescence of compound scorpioid cymes, these terminal at the ends of the main stem and lateral branches, densely glandular and hirsute, the individual cymes congested, but loosening in fruit, up to 10 cm long, pedicels up to 1.5 mm long; sepals spatulate to oblanceolate, 3.5-4.5 mm long, 0.7-1.7 mm wide, hirsute and stipitate-glandular; corolla campanulate, purplish to blue, 5-6 mm long and broad, pubescent; stamens exserted ca. 8-10 mm, filaments the same color as the corolla, anthers yellow; style exserted ca. 8 mm, bifid 3/4 its length, the lower 1/4 setose and glandular; capsule oval, 3-3.2 mm long, 2.9-3.1 mm wide, hirsute and glandular; mature seeds 4, oblong, brown ventrally to reddish dorsally, pitted, 2.8-3.4 mm long, 1.3-1.5 mm wide, the ventral surface lighter than the dorsal surface, the ridge corrugated on one side, the margins corrugated and more or less revolute. Collections: 15 (6); representative: D. Atwood 2591 (BRY, CAS); J. Howell 24397 (CAS); D. Atwood 2598 (ARIZ, B, BRY, CAS, COLO, DIXIE, GH, NY); D. Demaree 43982 (UC); D. Atwood 2601 (ASC, BRY, CAS, US, WSC).

HABITAT.— Red shale formation.

DISTRIBUTION.— Coconino Co., Arizona.

Phacelia welshii is probably most closely related to *P. utahensis* and *P. corrugata.* It can be distinguished from the former by its broader, dark brown seeds, long (up to 1.3 mm long), flattened, multicellular, stipitate glands, and broadly lanceolate leaves. The more open inflorescence, corrugated seeds, and broader, shorter, densely glandular leaves easily separate *P. welshii* from *P. corrugata.*

APPENDIX I

Synonyms

The following is a list of synonyms in the *Phacelia* Crenulatae group. The names in the left column are the synonyms, and the number to the right is the reference to the numbered taxa in the present treatment.

EUTOCA

E. glandulosa Hook.	17

PHACELIA

P. arenicola Brandegee	19a
P. conferta D. Don	10
P. congesta var. *dissecta* Gray	10
P. congesta var. *rupestris* (Greene) Macbride	29
P. congesta var. *typica* Voss	10
P. dissecta (Gray) Small	10
P. crenulata var. *ambigua* (Jones) Macbride	3a
P. crenulata var. *bakeri* Brand	7
P. crenulata var. *corrugata* (Nels.) Brand	12
P. crenulata var. *funerea* Voss in Munz	14b
P. crenulata var. *minutiflora* (Voss) Jeps.	3b
P. crenulata var. *vulgaris* Brand	14b
P. depauperata W. & S	26
P. deserta Nels.	17
P. foetida Goodding	24
P. glandulosa Gray in Brand. pro syn.	26
P. glandulosa Hemsley	13
P. glandulosa ssp. *eu-glandulosa* Brand var. *australis* Brand, in part	15
P. glandulosa ssp. *eu-glandulosa* Brand var. *australis* Brand, in part	7
P. glandulosa ssp. *eu-glandulosa* Barnd var. *deserta* Brand	17
P. glandulosa ssp. *eu-glandulosa*	1
P. glandulosa ssp. *splendens* (Eastwood) Brand	32
P. glandulosa var. *neomexicana* (Thurber ex Torr.) Gray	22
P. integrifolia var. *arenicola* (Brandegee) Brand	19a
P. integrifolia var. *palmeri* (Torr. ex Wats.) Gray	24
P. integrifolia var. *robusta* Macbr.	28
P. intermedia Wooton, in part	9
P. invenusta Gray	9

P. macdougalli Heller in Brand, pro. syn. 31
P. neomexicana var. *alba* (Rydberg) Brand .. 1
P. neomexicana var. *coulteri* (Greenman) Brand 13
P. neomexicana var. *coulteri* subvar. *folisissima* Brand 1
P. neomexicana var. *eu-neomexicana* Brand 22
P. neomexicana var. *microphylla* Brand 15
P. palmeri var. *typica* Voss 24
P. petiolata Johnston 23
P. popei var. *arizonica* (Gray) Voss 6
P. popei var. *similis* (W. & S.) Voss 26
P. popei var. *typica* Voss 26
P. similis W. & W. 26
P. tenuipes W. & S. 8
P. texana Voss 19b

Appendix II

Glossary

Alveolate. Honeycombed; pits in the surface of the seed.
Auriculate. With earlike appendages.
Corrugated. Wrinkled or folded.
Cymbiform. Boat shaped.
Cyme. A determinate flower cluster in which the first flower is terminal on the main axis and the central flowers open first.
Denticulate. Slightly and finely toothed.
Favose. Honeycombed; pits in the surface of the seeds.
Fimbriate. Fringed with elongate, slender processes or lobes on the margins of the corolla lobes.
Geminate. In pairs, as regarding the seeds.
Glandular. A globose-secreting structure borne on the surface and estipitate.
Gypsiferous. Containing gypsum.
Hirsute. Pubescent with stiff, coarse hairs.
Hispid. Pubescent with long, very stiff hairs, these able to penetrate the skin.
Pilose. Pubescent with soft, slender hairs pointing the same direction as if combed.
Pitted. Having little depressions or pits.
Puberulent. Pubescent with very short hairs, not stiff.
Reticulate. Net-veined.
Revolute. Rolled backward from both margins, toward the inside.
Scabrous. Rough to the touch owing to the presence of short stiff hairs.
Scarious. Thin, dry, and membranous, not green.
Scorpioid. A unilateral inflorescence circinately coiled in bud and anthesis.
Setose. Pubescent with short, rather stiff hairs, these not able to penetrate the skin.
Stipitate-glandular. A globose, stipitate, secretory structure borne on the surface of vegetative parts.
Strigose. Pubescent with short, straight appressed hairs.
Tuberculate. Having small knoblike projections.
Villous. Pubescent with long and weak, tangled, but not matted, hairs.

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RODENT POPULATIONS, BIOMASS, AND COMMUNITY RELATIONSHIPS IN *ARTEMISIA TRIDENTATA*, RUSH VALLEY, UTAH

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Abstract.— Three desert *Artemisia tridentata* communities in Rush Valley, Utah, were trapped for small rodents during the summer of 1970, and population densities were estimated for each population category using Lincoln's index. Animals were weighed and rodent biomass calculated by species throughout the summer. Population, biomass, and other data were then analyzed to gain an understanding of the community relationships of the three study areas to each other as well as to the *A. tridentata* community types of the Great Basin.

Peromyscus maniculatus, *Eutamias minimus*, and *Reithrodontomys megalotis* were common to area 1, whereas *P. maniculatus*, *E. minimus*, and *Perognathus parvus* were common to areas 2 and 3. The peak estimated standing crops were 182.8 (74.0), 143.1 (57.9), and 129.7 g/acre (52.5 g/ha) for areas 2, 1, and 3 respectively. The population and biomass of area 2 peaked in midsummer, area 1 early summer, and area 3 late summer.

Introduction

Big sagebrush (*Artemisia tridentata* Nutt.) covers an estimated total area of 226,364 square miles (586,283 km^2) in the Great Basin and associated areas of the western United States (Beetle, 1960) and is the most abundant plant species over much of this area. According to Hironaka (1963), "*A. tridentata* has the widest distribution of all the sagebrushes and occurs across the entire moisture gradient of the sagebrush zone." Passey and Hugie (1962) found *A. tridentata* occupying a greater number of soil types than any other sagebrush species.

A. tridentata is ecologically significant in that it provides not only food and cover for some species but competes against other desirable food and cover species. For economic reasons, however, many people consider sagebrush to be a highly undesirable plant. As a result, much research done in the sagebrush community has been directly concerned with controlling its spread and decreasing its abundance. Treatment resulting from such research has sometimes been temporarily effective. Some treated areas after 14 years may have more sagebrush on them than adjacent untreated areas (Johnson, 1969). The mean useful life cycle of spraying projects throughout Wyoming has been estimated to be about 15 years (Kearl, 1965).

The economic importance and ecological impact of such control measures make research leading to an understanding of the *A. tridentata* community imperative. The objective of this study is to establish baseline data by estimating the comparative small rodent density and biomass of *A. tridentata* communities in low-intermediate- and high-altitude desert areas of the Great Basin and using this estimation to compare the three communities.

Rush Valley, Utah, was chosen for the area of research because (1) it is a designated grazing research area of the Intermountain Forest and Range Experimental Station, which funded the project; (2) a large part of the valley is covered by *A. tridentata;* (3) the data gathered will augment that of current and past research in the valley; and (4) the data collected will aid future studies and management of the valley.

No literature relating rodent density with biomass or energy flow has been published concerning sagebrush communities. There are works, however, that have been reported for other terrestrial communities. Densities of rodents have been studied in Rush Valley, Utah, primarily in pinyon-juniper and reseeded areas (Baker, 1969). Woodbury (1955) reported on the small mammal distribution in Cedar Valley which borders Rush Valley on the east. Vest (1962) reported on the small mammal distribution in Dugway Valley which borders Rush Valley on the west. Rodents of sagebrush communities in both valleys were discussed.

Although literature concerning biomass in *A. tridentata* communities is sparse, much descriptive material is available on the plant and its community type. A morphological life history of *A. tridentata* was written by Diettert (1938), and Beetle (1960) published a taxonomic and distributional study of all the north American sagebrush taxa. Other references concerning *A. tridentata* communities in Utah may be found in Christensen (1967).

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MATERIALS AND METHODS

Study Areas

Three 14.5 acre (5.87 ha) study areas located in the southern part of Rush Valley, Tooele County, Utah, were selected and are described in Table 1. Area 1, elevation 5,100 feet (1,554 m), is located in the southwest quarter of Section 10, Township 7 south, Range 5 west, Tooele County, Utah. It contains irregularly scattered *A. tridentata* interspersed with *Chrysothamnus puberulus*, the grass *Distichlis stricta*, and bare ground. *Distichlis stricta*, an indicator of alkaline soil conditions, is abundant in a number of small areas with poor drainage as are numerous *A. tridentata* plants 1-3 inches (2.5-7.6 cm) tall. This short sagebrush is possibly stunted by an accumulation of soil salts. The area has a wash 1-2 feet (0.3-0.6 m) deep and five feet (1.5 m) wide that runs across the west side.

Area 2, elevation 5,700 feet (1,737 m) is located in the northwest quarter of Section 35, Township 8 south, Range 6 west, Tooele County, Utah, and is characterized by scattered *A. tridentata* with some *Sarcobatus vermiculatus* and much bare ground. The west boundary of this area is a dirt road, beyond which there is an extensive stand of *S. vermiculatus* mixed with the grass *Agropyron cirstatum.*

Area 3, elevation 6,500 feet, (1,981 m) is located in the west half of Section 4, Township 9, Range 5 south, Tooele County, Utah, and is covered with irregularly scattered *A. tridentata* with a dense understory of a perennial lupine and various grasses, principally *Agropyron dasystachyum* and *Sitanion hystrix.* There is little bare ground except on the east and west borders which were exposed when adjacent land was cleared of *A. tridentata* and some *Juniperus osteosperma* in the fall of 1969.

Vegetation sampling on all areas consisted of measuring (1) absolute ground cover, (2) percent species cover composition, (3) frequency and density of perennial species other than grasses, (4) frequency of all grasses, both annuals and perennials, lumped together, and (5) frequency of all annuals, except grasses, lumped together. A modified line-point method of sampling was used to determine cover, and small quadrats were used for frequency and density data collection (Cain and Castro, 1959). These data are available in Nicholes (1972).

TABLE 1. General comparisons of the study areas.

Characteristics	Area 1	Area 2	Area 3
[1]SOIL TYPE	deep silt-clay alkali soils of the arid & semi-arid valley bottoms	deep silt-loam soils of the semiarid valley bottoms	deep, loamy, dry soils of the dry subhumid alluvial fans
Slope	0-2%	1-5%	1-25%, most less than 10%
Water runoff	slow	slow to medium	slow to medium
Erosion	slight to moderate	high	moderate
[1]CLIMATE			
Mean annual temp.	51 F	48 F	45-47 F
Mean annual prec.	8-10 inches	8-12 inches	12-15 inches
PRINCIPAL COVER	*Artemisia tridentata* *Chrysothamnus puberulus* *Distichlis stricta*	*Artemisia tridentata* *Sarcobatus vermiculatus* various grasses	*Artemisia tridentata* Lupine sp. various grasses
PRINCIPAL RODENTS	*Peromyscus maniculatus* *Eutamias minimus* *Reithrodontomys megalotis*	*Peromyscus maniculatus* *Eutamias minimus* *Perognathus parvus*	*Peromyscus maniculatus* *Eutamias minimus* *Perognathus parvus*
ELEVATION	5.100 ft. (1,554 m)	5.700 ft. (1.737 m)	6.500 ft (1.981 m)

[1](Harvey and Woodward, 1969)

Trapping

Each of the quadrat study areas, 14.5 acres (5.87 ha), was equally divided into 25 squares with a trap station located in the center of each square where three Sherman aluminum live traps were placed. The trapping stations were 160 feet (48.8 m) apart. Rolled oats were used as bait. The traps were set in the afternoon, checked each morning, and closed until the afternoon resetting. Each trapping period covered five consecutive nights, every other week from 2 June to 14 August 1970 (Table 2). The three areas were trapped simultaneously for six trapping periods. To offset bias prior to each trapping period, the sequence in which each of the three areas would be checked and reset was determined randomly. This sequence was maintained throughout a trap period.

At the end of six trapping periods each area was "kill trapped" to compare with live trapping success during the previous periods. A "kill trapping" consisted of one night of live trapping with one live trap set at each of the regular trapping stations, one live trap placed at the corners of each square, and one live trap placed at the middle of each side of the squares, for a total of 121 traps. Before the second trap night each live trap was replaced by two museum special snap traps for a total of 242 traps per quadrat. This trapping pattern continued three to four nights until the number of previously marked animals caught was reduced to none or nearly none. The "kill trapping" did not occur simultaneously for each area because of the large number of traps involved (Table 2).

Animals were toe clipped for identification. Data recorded for each individual animal handled during the study included (1) species, (2) sex, (3) age, (4) weight, (5) trapping station, and (6) notes concerning the animal's general condition, such as pregnancy, parasitism, injuries, and others. Age classes of juvenile, subadult, and adult were determined primarily by pelage color and molt patterns; but the appearance of genitals, behavior of animals, and, in cases where age is extremely difficult to determine, i.e., chipmunks, the weights of the animals were considered. Animals were weighed using a spring-operated scale accurate to the nearest 0.5 g.

TABLE 2. Schedule of trapping periods.

[1]Dates	Areas 1	2	3
Live Trapping			
1. 2-6 June	X	X	X
2. 15-19 June	X	X	X
3. 29 June-3 July	X	X	X
4. 13-17 July	X	X	X
5. 27-31 July	X	X	X
6. 10-14 Aug.	X	X	X
"Kill Trapping"			
7. 24-27 Aug.	X		
8. 31 Aug.-4 Sept.			X
9. 6-9 Sept.		X	

[1] Dates extend from the first morning traps were checked to the last morning traps were checked during a trap period.

Population and Biomass Estimation

For each species caught and recaptured in sufficient numbers, population estimates were made at the end of each trapping period using Lincoln's, Hayne's, and Jolly's indices (Giles, 1969). Estimates were made for (1) the total species population, (2) the population of each age class within the species, and (3) the population of each sex within the species. Nichols (1972) presents this data. Comparison of the three estimators showed Lincoln's and Hayne's to be similar, but Lincoln's estimates were used in the biomass calculations. Population estimates for "kill trapping" periods were made after the first two nights of trapping, since two nights of "kill trapping" may have caused abnormal immigration into the areas. All other population estimates were calculated using five days of live trapping data.

Species biomass was calculated by multiplying the mean species weight by the estimated population number of that species for each trapping period. Previous experience had shown that animals repeatedly caught during a trapping period tended to lose weight, likely due to trapping stress. To compensate for this, the mean weights were calculated two different ways: (1) using only the weight of an animal taken the first day during a given trapping period and (2) using the weight of an animal taken every day during its captivity for a given trapping period. The greatest of these mean weights for any population category was used in this study. In most instances method one was used.

RESULTS

Four species of rodents were recaptured in sufficient numbers to be considered in detail, but only three were prevalent in any given area. These species were—

	Area 1	Area 2	Area 3
Peromyscus maniculatus	X	X	X
Perognathus parvus		X	X
Reithrodontomys megalotis	X		
Eutamias minimus	X	X	X

The Lincoln population estimate for each species caught during each trapping period and study area is given in Table 3. The combined total number of rodents estimated, of all species considered, for each area is graphically shown in Figure 1. The following is a general breakdown of each area's trapping according to species. Detailed charts and tables of data are given in Nichols (1972).

Area 1

Peromyscus maniculatus. The greatest number of *P. maniculatus*, 47 (Lincoln's estimate 50), appeared during trap period 3 with a male-female ratio of nearly 2:1. There were 16 juveniles, 30 subadults, and 1 adult. The least number, 24 (Lincoln's estimate 25), composed of 3 juveniles, 17 subadults, and 4 adults with a male-female ratio of 5:3, appeared during period 1. The greatest mean species weight, 19.6 g, occurred during period 1 and the least, 15.5 g, during period 5.

Reithrodontomys megalotis. In area 1 *R. megalotis* was captured least often of the main species. The greatest number, 14 (Lincoln's estimate 18), appeared during period 2 with a male-female ratio of 3:4. There were no juveniles, 2 subadults, and 12 adults. During periods 4, 5, and 6 no mice of this species were caught. The greatest mean species weight, 13.9 g, occurred in period 3 and the least, 11.1 g, in period 2.

Eutamias minimus. The greatest number of *E. minimus*, 33 (Lincoln's estimate 33), appeared during period 1 with a male-female ratio of approximately 3:2. There were 16 juveniles, 14 subadults, and 3 adults. The least number, 10 (Lincoln's estimate 8), composed of 0 juveniles, 9 subadults, and 1 adult with a male-female ratio of nearly 1:1, appeared during period 6. The greatest mean species weight, 30.5 g, occurred during period 5 and the least, 28.4 g, during period 4.

Area 2

Peromyscus maniculatus. The greatest number of *P. maniculatus*, 49 (Lincoln's estimate 43), appeared during trap period 6 with a male-female ratio of nearly 3:2. There were 5 juveniles, 38 subadults, and 6 adults. The least number, 13 (Lincoln's estimate 12), composed of 6 juveniles, 5 subadults, and 2 adults with a male-female ratio of 5:8, appeared during period 2. The greatest mean species weight, 18.2 g, occurred during period 5 and the least, 15.3 g, during period 1.

Perognathus parvus. In area 2 *P. parvus* was captured least of the three main species. Both periods 5 and 6 yielded the greatest number, 10 (Lincoln's estimates 9 and 10), with male-female ratios of 7:3 and 3:1. The respective age distributions were 0 and 2 juveniles, 9 and 7 subadults, 1 and 1 adults. The period of least capture was period 1 when one adult female was captured. The greatest mean species weight, 18.7 g, occurred during period 2 and the least, 14.5 g, during period 3.

Eutamias minimus. The greatest number of *E. minimus*, 43 (Lincoln's estimate 46), appeared during period 2 with a male-female ratio of approximately 4:3. There were 20 juveniles, 16 subadults, and 7 adults. The least number of chipmunks, 14 (Lincoln's estimate 13), composed of 1 juvenile, 12 subadults, and 1 adult with a male-female ratio of nearly 4:1, appeared during period 3. The greatest mean species weight, 31.1 g, occurred during period 5 and the least, 27.7 g, during period 1.

Area 3

Peromyscys maniculatus. The greatest number of *P. maniculatus*, 55 (Lincoln's estimate 49), appeared during trap period 3 with a male-female ratio of approximately 3:5. There were 16 juveniles, 31 subadults, and 8 adults. The least number, 29 (Lincoln's estimate 26), composed of 2 juveniles, 18 subadults, and 9 adults with a male-female ratio of 3:4, appeared during period 1. The greatest mean species weight, 19.9 g, occurred during period 1 and the least, 17.5 g, during period 6.

Perognathus parvus. The greatest number of *P. parvus*, 47 (Lincoln's estimate 54), appeared during period 6 with a

TABLE 3. Estimated population numbers and biomass for the three study areas.

		Lincoln's $\widehat{\underline{N}}$ no./14.5 acres (5.86 ha)			Estimated biomass (g/14.5 acres) (5.86 ha)		
Trap Period	Species	Area 1	Area 2	Area 3	Area 1	Area 2	Area 3
1	P.M.	25	18	26	490.0	275.4	517.4
	E.M.	33	34		943.8	941.8	
	P.P.			25			530.0
	R.M.						
		58	52	51	1433.8	1217.2	1047.4
2	P.M.	44	12	36	752.4	199.2	698.4
	E.M.	39	46		1123.2	1311.0	
	P.P.		1	40		18.7	836.0
	R.M.	18			199.8		
		101	59	76	2075.8	1528.9	1534.4
3	P.M.	50	16	49	875.0	283.2	886.9
	E.M.	31	13		914.5	374.4	
	P.P.		2	29		29.0	559.7
	R.M.	1			13.9		
		82	31	78	1803.4	686.6	1446.6
4	P.M.	48	26	55	811.2	434.2	1078.0
	E.M.	23	28		653.2	848.4	
	P.P.		8	36		148.0	655.2
	R.M.						
		71	62	91	1464.4	1430.6	1733.2
5	P.M.	41	27	58	635.5	491.4	1044.0
	E.M.	5	24	2	152.5	746.4	68.4
	P.P.		9	38		162.9	767.6
	R.M.						
		46	60	98	788.0	1400.7	1880.0
6	P.M.	35	43	47	591.5	722.4	822.5
	E.M.	8	59		242.4	1770.0	
	P.P.		10	54		158.0	1015.2
	R.M.						
		43	112	101	833.9	2650.4	1837.7
7	P.M.	33			488.4		
	E.M.	12			337.2		
		45			825.6		
8	P.M.			43			705.2
	E.M.			3			91.5
	P.P.			47			794.3
				93			1591.0
9	P.M.		61			1067.5	
	P.P.		6			85.2	
			67			1152.7	

Key: P.M.—*Peromyscus maniculatus;* E.M.—*Eutamias minimus*. P.P.—*Perognathus parvus*. R.M.—*Reithrodontomys megalotis.*

male-female ratio of approximately 7:5. There were 4 juveniles, 21 subadults, and 22 adults. The least number, 19 (Lincoln's estimate 25), composed of 0 juveniles, 3 subadults, and 16 adults with a male-female ratio of nearly 2:1 appeared during period 1. The greatest mean species weight, 21.2 g, occurred during period 1 and the least, 18.2 g, during period 4.

Eutamias minimus. In area 3 *E. minimus* was captured the least of the three main species. The greatest number, 6 (Lincoln's estimate 0), appeared during period 6 with a male-female ratio of 1:2. There were 0 juveniles, 3 subadults, and 3 adults. No chipmunks were caught during period 3. The weight, 39.0 g, of one adult female, the only animal caught during period 1, represents the greatest mean species weight. The least mean species weight was 29.5 g and occurred during period 3.

Estimated Small Rodent Biomass

The estimated biomass of each species for every period and study area, along with total biomass per area, is given in Table 3. In addition Table 3 lists the Lincoln population estimates used in the biomass computations. Kill-trap data were not included in calculating the greatest, least, and mean area biomass as given in the following description of rodent biomass by areas, but they are included in Table 3. The kill-trap biomass for any of the three areas fell within the limits of the estimates for that particular area from the six previous trapping periods.

Area 1. The greatest estimated small rodent biomass, 143.1 g/acre (57.0 g/ha), for area 1 occurred during period 2. The least, 54.3 g/acre (22.0 g/ha), occurred during period 5. The mean biomass of area 1 over the six trapping periods was 96.5 g/acre (39.1 g/ha). The mean was approached during periods 1 and 4. Periods 5 and 6 were well below the mean as was kill-trap period 7.

Area 2. The greatest biomass, 182.8 g/acre (74.0 g/ha), for area 2 occurred during period 6. The least, 47.4 g/acre (19.2 g/ha), occurred during period 3. The mean biomass of area 2 over the six trapping periods was 102.5 g/acre (41.5 g/ha). The mean was approached during periods 2, 4, and 5. Area 2 had the greatest and the lowest biomass of all three areas during the study.

Area 3. The greatest biomass, 129.7 g/acre (52.5 g/ha), for area 3 occurred during period 5 and the least, 72.2 g/acre (29.2 g/ha), occurred during period 1. The mean biomass of area 3 over the six trapping periods was 109.9 g/acre (44.5 g/ha). The mean was approached during period 2 and kill-trap period 8.

DISCUSSION

To understand an *A. tridentata* community a knowledge of the associated vertebrates and vegetation must be obtained. An analysis of each *A. tridentata* study area is thus important in a discussion relating the rodent population and biomass of the individual areas to each other to establish the picture for the community type.

Peromyscus maniculatus and *E. minimus* were two of the three predominant rodent species in each area. This could be expected for *P. maniculatus* because of its geographic range over most North American biomes (Burt and Grossenheider, 1964; King, 1968), including sagebrush regions of the Great Basin. *Eutamias minimus* also has a broad geographical range, including the Great Basin and much of Canada. Its appearance on all study areas should also be expected since it is characteristic of sagebrush communities (Gordon, 1943; Burt and Grossenheider, 1964). Out of 43 vertebrate species noted during the study, 15 were common to all three areas, an indication that the study areas were similar. Table 1, however, indicates that notable differences existed between them. These differences resulted from the distribution of the 28 vertebrates which were not common to the three areas (Nichols, 1972). Area 1 had 4, area 2 none, and area 3 12 unique species of vertebrates present. The large number of unique species for area 3 can be explained by the presence of a more diverse habitat than in the other areas. This diversity was likely due to more favorable climatic and edaphic factors (Table 1). Area 2 was intermediate in soil, slope, temperature, and precipitation (Table 1). The lack of vertebrate species unique to area 2 also indicates that it was an intermediate area.

Area 1 exhibited the least vertebrate diversity, area 2 was transitional but closer to area 1, and area 3 was the most diverse. Most of the rodent biomass for areas 1 and 2 came from *E. minimus*, while their contribution in area 3 was small (Table 3). This supports the apparent closer relationship of area 2 to area 1. It should also be kept in mind that areas 1 and 3 are the farthest apart geographically and altitudinally, with area 1 (elev. 5,100 ft.; 1,554 m) near the valley floor, area 3 (elev. 6,500 ft.; 1,981 m) at the base of the valley-forming mountains, and area 2 (elev. 5,700 ft.; 1,737 m) on the benchland between them.

The ground cover of each area was dominated by *A. tridentata*, although each area had a different predominant understory species (Nichols, 1972). The diversity pattern reflected was one of low plant species diversity for areas 1 and 2 and high diversity for area 3. Area 1 had 14, 2 had 15, and 3 had 30 plant species present. This was similar to the vertebrate diversity pattern for the respective areas. This similarity in vertebrate and plant diversity patterns was likely due to the edaphic and climatic factors affecting the plants which in turn affected the vertebrates. The lack of complete similarity between vertebrate and plant patterns, however, may have been due to the physiognomic differences of the cover species present in the areas rather than the amount of diversity.

It is suggested that the amount, distribution, and physiognomy of dominant vegetative cover in *A. tridentata* communities may have a greater influence than the diversity of cover species in determining vertebrate presence. Turner (1950) supports this idea, especially for *Peromyscus* distribution, in his study of 10 vegetative types, including 3 having *A. tridentata* as the dominant or codominant plant. Rosenzweig and Winakur (1969) have hypothesized from studies in the lower-Sonoran desert scrub vegetation that "the spatial variations in density of some species [rodent] are responses to spatial characteristics of their environment. Important among these environmental characteristics tend to be measures of the presence and/or absence of vegetation of various physiognomies."

The absolute cover of *A. tridentata* in area 1 was 17.6 percent; 2 was 15.5 percent; and 3 was 23.2 percent. Percent cover composition was 44.2 percent (area 1), 48.0 percent (area 2), and 38.0 percent (area 3). Area 2 had the least absolute cover of *A. tridentata* with the most bushes less than 2 feet (0.6 m) high but had the greatest percent cover composition of *A. tridentata* for the three areas. This cover pattern may have been why area 2 had no unique vertebrates, thus functioning as a limiting factor to diversity. Area 1 had four species but was no more diverse than area 2 in terms of plant species, indicating that in this case cover type had a greater effect than did plant diversity. Area 3, in terms of *A. tridentata* cover, was opposite area 2. Area 3 had the greatest absolute coverage of *A. tridentata* with most bushes greater than 2 feet (0.6 m) high but had the least *A. tridentata* cover composition for the areas. This showed the opposite effect on vertebrate presence than the pattern in area 2. Instead of having no unique vertebrate species as in area 2, there were 12, including 2 rodents. The relationship for area 3, however, was not as pronounced because that area had nearly twice the plant species diversity of areas 1 and 2; and the greater plant species diversity may be responsible for the greater vertebrate diversity. If this is true, it is a direct reversal of the results obtained by Rosenzweig and Winakur (1969) in the lower-Sonoran desert scrub vegetation. They found that "the variation in plant species diversity failed to explain the variation in animal species diversity and that some of the most faunally diverse areas had the fewest species of plants." The three areas reported in this study, however, are in the Great Basin cold desert, which varies considerably from the Sonoran hot desert. It is possible that the amount and distribution of *A. tridentata* cover is only important in determining vertebrate distribution in areas with low total absolute cover as in areas 1 and 2 but not in area 3.

According to Pearson (1965a, 1965b) and Beatley (1969), primary productivity of *A. tridentata* communities peaks in late spring and early summer. Peaks in rodent populations in *A. tridentata* communities occur during the early summer to fall period (Turner, 1950; Sullivan, 1961). Trojan (1970) has shown that in a Polish grassland the rodent biomass increase during the summer is four times as great as during the winter and two times as great as during the spring. Summer and autumn increases accounted for 89 percent of the annual increase. He stated that "winter increases are of almost no importance to assessment of energy flow (3.2 percent)." His results may be applicable to the Great Basin sagebrush zone because its increased elevation could partially compensate for the higher latitude and much lower elevation of Poland. The Polish study was done in a grassland, but the areas studied in Rush Valley, Utah, were probably grassland before the valley's settlement (Christensen and Hutchinson, 1965). Winter production may be important in some sagebrush areas, but no winter data were taken in this study due to inaccessibility.

If (1) the annual peak primary production of *A. tridentata* communities was late spring and early summer, (2) rodent populations in *A. tridentata* communities peaked in the early summer to fall, and (3) there was little increase in rodent biomass during the previous winter months, then the population, mean species weights, and biomass data collected during this study should illustrate the dynamic relationships of the three study areas.

Estimated Populations

The total population estimates of all species are shown in Table 3 and Figure 1. Area 1 had a definite early summer population peak followed by a steady decline and a leveling off in the fall, but area 3 had three different population peaks during the summer with the highest population occurring in late summer (approx. August 13). Area 3 had a gradual increase in rodent numbers, peaking in late summer (approx. August 13) and declining by September 3.

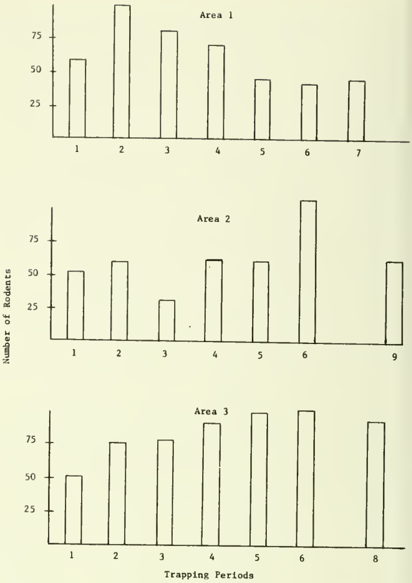

Fig. 1. Number of rodents estimated in all areas.

Mean Species Weights

Mean species weight is not only important in calculating the estimated rodent biomass, but Walkowa (1970) pointed out the importance of species weights as an exploitation compensation mechanism in rodent populations. He found that reproduction operates as a compensating mechanism only if exploitation exceeds 31 percent. When exploitation was 0-30 percent, an increase in exploitation caused an increase in the production of biomass. In this study there appeared to be no unusual predatory or disease exploitation of populations above 30 percent; thus the species were likely reacting to exploitation by increasing biomass without increasing reproduction. This was further evidenced by the lack of high-population densities. The greatest estimated rodent density was eight rodents per acre (3.24 ha) in area 2 during its summer peak.

In addition to rodent weights varying with population exploitation, they also vary with the animal's daily activities. Tevis (1955) showed that the gross body weight increase in chipmunks going from an empty stomach to a full stomach averaged 6-8 percent, whereas Evans (1949) observed that voles increased 20 percent in body weight within five minutes after water consumption. It is evident, therefore, that an accurate biomass estimation requires use of weights from the particular time and population being considered. Mean species weights used in this study were calculated from what was believed to be the most accurate weight according to the above criteria, but errors may have occurred.

Area 1. The mean species weight of *P. maniculatus* was greatest in the early spring and then oscillated between lower weights throughout the study. The high weight during period 1 reflected the population structure at that time. There were few juvenile and subadult animals compared with subsequent periods. After period 1 there were increased numbers of juveniles emerging from the nests, causing a sharp decrease in mean species weight during trap period 2. For the remainder of the study reproduction caused oscillations in the mean species weights between trapping periods. These oscillations were expected since *P. maniculatus* is polyestrous (Asdell, 1964). The *E. minimus* mean species weights generally appeared to increase throughout the study to a peak near the end of the summer during trap period 5. This increase paralleled a gradual decrease in population numbers throughout the summer. The *E. minimus* reproductive pattern, one litter in the spring and subsequent growth of the young during the summer (Asdell, 1964), was responsible for the inverse relationship. No pattern was evident for *R. megalotis* because of insufficient captures.

Area 2. The mean species weight pattern of *P. maniculatus* in area 2 oscillated for the same reason as their observed oscillations on area 1, but the greatest mean species weight occurred in period 5. There was an apparent slow period in reproductive activity during June and July compared with area 1. This undoubtedly allowed the summer mean species weight of the population to peak later than in area 1. The mean species weights of *E. minimus* gradually increased during the summer because of their reproductive pattern. Too few *P. parvus* were caught in this area to show any definite patterns, but the same slow reproductive activity as noted in *P. maniculatus* on this area was also noted for *P. parvus*.

Area 3. The mean species weight pattern of *P. maniculatus* showed reproduction occurring throughout the summer. The *P. parvus* pattern in area 3 showed increased population numbers associated with decreased mean species weights throughout the study. This was expected since *P. parvus* is polyestrous (Asdell, 1964). Too few *E. minimus* were caught on this area to show any definite pattern.

Biomass

The total estimated seasonal biomass in each area (Table 3 and Fig. 2) was similar to the population estimate for the area (Fig. 1). In terms of biomass, however, there was clearly a closer relationship between areas 1 and 3 than had previously been proposed. Biomass in area 2 showed that secondary production was rather unstable compared with areas 1 and 3.

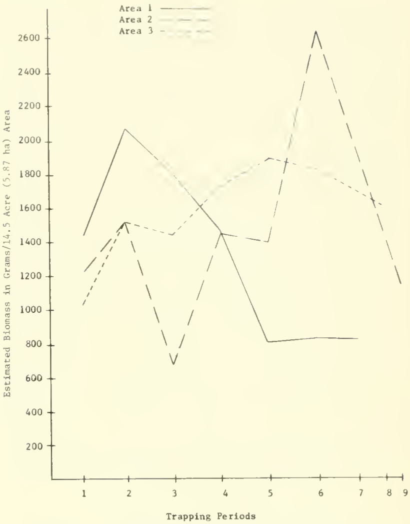

Fig. 2. Estimated total small rodent biomass by trapping periods.

Area 1. An early summer increase of 50 percent in rodent biomass was evidenced in area 1 during a 13-day interval between trap periods 1 and 2, which made trap period 2 appear as the peak period of summer rodent biomass production for area 1 (Fig 2). There was then a steady drop in biomass over a 42-day period followed by a leveling off. The data indicates, however, that the number of *E. minimus* and *R. megalotis* may have been overestimated during period 2. There were 39 *E. minimus* estimated during period 2, but only 29 were handled. There were also 4 more *R. megalotis* estimated than were actually handled. A high number of unmarked animals being caught at the end of a trap period would cause a high unmarked-to-marked animal ratio to occur. This high ratio would in turn cause an overestimation of the population. This high ratio may be caused by immigration of animals into the area, by new animals emerging from their nests, or by various other factors. In this instance the possible overestimation may have been caused by new juvenile male chipmunks becoming available to the traps.

If the actual number of rodents handled

during period 2 is used in the biomass calculation, then the summer peak on area 1 did not occur during trap period 2 but during trap period 3. The possible correction is shown in Figure 3. The total pattern for the summer, however, is still one of an early peak in rodent biomass followed by a steady drop and then a leveling off for the remainder of the study. This is what could be expected for a community in poor soil with low plant species diversity, as area 1 was earlier shown to be. Secondary production peaked early in the summer, after the observed peak primary production, thus placing greater demands upon the primary production of the community to support the increased secondary production. The plant community, beyond its peak production and with very little diversification, likely could not produce more food for the increased rodent population, so the rodent population rapidly declined to a level reflecting the probable carrying capacity of the community and then remained there through the end of the summer. Because of poor soil and other factors, the carrying capacity was low, approximately 55 g of rodent biomass per acre (22.27 g/ha). This low carrying capacity could have supported no more than one *E. minimus* and one *P. maniculatus* per acre (.24/ha).

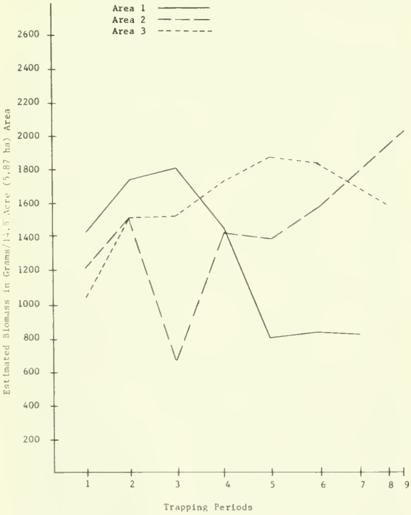

Fig. 3. Estimated total small rodent biomass by trapping periods using possible corrections.

Area 3. The rodent biomass of area 3 showed an entirely different pattern than area 2 throughout the summer (Fig. 2). Secondary rodent productivity increased rapidly after spring reproduction and was then followed by a short period of reduction before rising again. This reduction may have been due to a number of factors but was most likely caused by cold temperatures. The *P. parvus* estimate for the period of biomass drop (trap period 3) was considerably less than the previous estimate. This rodent, as a protective behavioral adaptation, regularly goes into a state of torpor when it encounters cold (Bartholemew and Cade, 1957; Beer, 1961; Morrison and Ryser, 1962; Chew et al., 1965, 1967; Tucker, 1962, 1963, 1965a, 1965b, 1966). During the second and third nights of trap period 3 the coldest summer temperatures were recorded for area 3, and four *P. parvus* that probably would have been caught had the nights been warmer were not recaptured. This could have led to a low population estimate and thus a low biomass estimate for the period. If this were the case, then the biomass of area 3 would have shown an increase from trap period 1 to its peak in trap period 5. The possible correction is shown in Figure 3. At the end of the summer peak biomass gradually declined. Because of the diversity of the plant community in area 3, favorable climatic conditions and primary production were probably sufficient to supply food for the gradual summer increase in secondary production.

Area 2. The graphing of rodent biomass for area 2 showed no pattern similar to areas 1 or 3. It did, however, show an early summer decline in standing crop, a rapid recovery with leveling off for a trap period, a midsummer biomass increase to a peak higher than in either areas 1 or 3, and a late summer decline in standing crop of the same rate as that which occurred in the early summer.

Close examination of the data, however, for the *E. minimus* population showed a large trap mortality during period 6. This caused Lincoln's index to overestimate the population. It estimated 20 more *E. minimus* than were actually handled, which would represent an overestimation of 1,060.5 g in biomass. Thus, at trap period 6 the high peak shown in Figure 2 would probably be much lower. The possible correction is shown in Figure 3. With this correction the biomass was below that of area 3 for the same period.

Closer examination of the data revealed another possible error. In trap period 9 there were 29 different *E. minimus* handled, but because this period was a kill-trap period, the diurnal chipmunks were not caught during the one live trap night. As a result, none were marked, and no population estimates were made on day 2 of the kill-trap period. There were 17 different chipmunks handled on days 1 and 2 of this period. If the biomass of these rodents were added to the total biomass of this period, it would raise the total by 879.7 g. This possible correction is also shown in Figure 3.

The above corrections change considerably the estimated summer biomass pattern of area 2. The pattern now becomes one of an early summer decline in biomass, a recovery period, a period of no increase or decrease in biomass, and a steady rise in biomass that may not have peaked before the study ended. In terms of stability the community of area 2 appeared to be less stable than those of areas 1 and 3. The corrected pattern showed that in terms of biomass area 2 was more similar to area 3 than area 1 as had been previously proposed.

CONCLUSIONS

It appeared that when the characteristics of (1) vertebrate presence and distribution, (2) plant presence and distribution, (3) comparative rodent population numbers, and (4) comparative rodent biomass of the areas were considered, the three areas were in three different climatic or edaphically induced successional stages or conditions. Area 2 had the least diverse vertebrate presence. This may have resulted from the *A. tridentata* cover being composed of small bushes representing the greatest percent cover composition of the three areas. Area 2 was the least stable in terms of the annual cycle for rodent populations and biomass increase, probably a result of the poor plant species diversity. Area 3 had the most diverse vertebrate presence and was the most stable in terms of the annual cycle for rodent population and biomass increase. This may have been due to the *A. tridentata* cover pattern, which was opposite that found in area 2, and/or to the increased plant species diversity found in area 3. Area 1 appeared to be intermediate, in its vertebrate presence and *A. tridentata* cover patterns, to areas 2 and 3. Its annual cycle in terms of rodent population and biomass increase showed the earliest peak of the three areas. This may have been due to poorer soil and climatic conditions causing an early peak in primary productivity, a subsequent early peak in rodent productivity, and an extended period through the rest of the summer when conditions did not favor either primary or secondary production.

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COMPUTERIZED REDUCTION OF METEOROLOGIC MEASUREMENTS FROM IRRIGATED AND NONIRRIGATED PLOTS IN CENTRAL UTAH[1]

Ferron L. Andersen[2] and Paul R. Roper[3]

Abstract.— Two FORTRAN IV computer programs were developed to facilitate reduction of meteorologic data from irrigated and nonirrigated plots at Provo, Utah. The first program compiles and tabulates daily, monthly, and yearly summaries of precipitation as rain and/or snow, snowfall, total snow cover, soil moisture, dew, relative humidity, potential evaporation, cloud cover, and wind. Temperature values are tabulated for measurements taken in a standard weather shelter, 5 cm beneath soil surface under grass cover, at soil surface under grass cover, and on bare ground.

The second program enables complete computerized (Calcomp) construction, labeling, and graphing of 10 different meteorologic measurements and 3 calculated comparisons of temperature means.

Advantages of the first computer program relate generally to that obviously noticeable with any computerized tabulation. Those of the second program relate more specifically to the greatly reduced cost of computerized graphs compared with those produced manually, as well as to the marked reduction of errors compared with the number frequently associated with the usual tedious and laborious plotting of voluminous weather data.

Meteorologic data collected for the year demonstrated the beneficial effect of irrigation in the creation of microenvironments for living organisms.

Introduction

A comparison of meteorologic measurements from irrigated and nonirrigated plots in Provo, Utah, for 1970 through 1972 was published recently by Andersen, Wright, and Fox (1974). Included in their report was a detailed description of the study area, instrumentation employed, method of handling meteorologic data, and a series of manually reproduced graphs depicting the results for those three years. The current report is designed as a companion article to the one referred to above. It extends the meteorologic measurements through 1973 for an adjacently located plot watered via sprinkling as opposed to flood irrigation used in the previous project. Furthermore, it emphasizes those changes that have been incorporated to enable the graphing of 10 different meteorologic measurements and 3 comparisons of calculated means by a Calcomp plotter.

The importance of irrigation in creating optimum microenvironments for biological organisms has been substantiated for such invertebrates as mosquitoes (Rainy and Hess, 1967; Reeves and Hammon, 1962), snails (World Health Organization, 1950), and nematode larvae (Furman, 1944; Honess and Bergstrom, 1966; Fox, Andersen, and Hoopes, 1970; and Wright and Andersen, 1972). The importance was elaborated upon further by Andersen et al. (1974) and, thus, will not be discussed here.

Description of Experimental Plot

The experimental plot measured 10 x 30 m and was located at the Brigham Young University Animal Science Farm, Provo, Utah, adjacent to the plot used in the study by Andersen et al. (1974). The coordinates of the station site, elevation, description of vegetative cover, soil type and drainage, instrumentation, and method of collecting data were the same as reported earlier. The plot was divided into an irrigated and a nonirrigated section separated by an elevated dike. Additional diking, aproximately 8 in (20 cm) high, was also placed around the upper border and sides of the plot to prevent any flood irrigation waters from entering the experimental area. Beginning in May the irrigated portion was sprinkled each Monday with a total of 1 in (2.5 cm) of water as measured in the rain gauge. This was applied at an approximate rate of 0.5 in/hr. In June the amount was increased to 1.5 in (3.25 cm) and in July to 2 in (5.0 cm). The amounts were reversed for August, September, and October, after which time sprinkling ceased. This regimen for 1973 added a total of 39 in (97.5 cm) of water to the irrigated plot over the six month period.

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[1] This project was supported in part by Public Health Service Grant AI 10588.

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Descriptions of Programs

Two FORTRAN IV programs, one for data tabulation and a second for Calcomp graphing, were developed for this project. Figure 1 outlines the collation and handling of meteorological data and Figures 2 and 3 illustrate flow charts for the data tabulation and Calcomp graphing programs respectively. All meteorologic data for the year were entered on specially designed worksheets (Figs. 4 and 5), keypunched on 80-column IBM cards, and handled as diagrammed. All mensural data not already in the metric system were so transposed by appropriate conversion formulae. Also, the printing of all negative or zero values was suppressed whenever such data were not meaningful.

The first program compiles and tabulates daily, monthly, and yearly summaries of all meteorologic data collected. Tables 1, 2, and 3 are sample printouts of one month's data (May 1973), and Tables 4 and 5 are the two-page annual summary sheets.

The second program developed for the project enables complete computerized

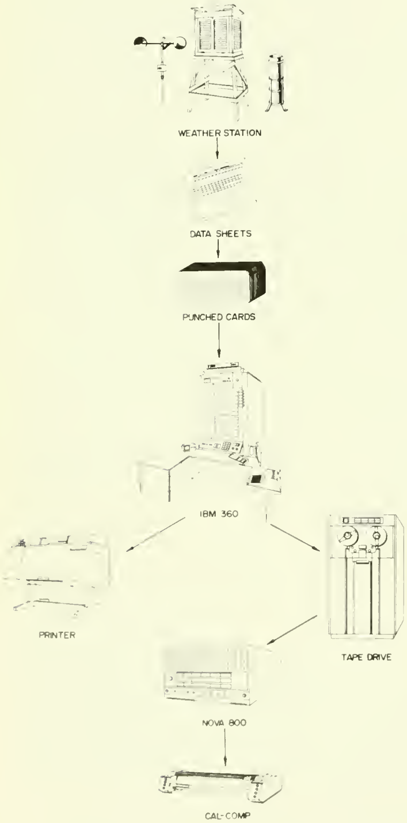

WEATHER STATION
DATA SHEETS
PUNCHED CARDS
IBM 360
PRINTER
TAPE DRIVE
NOVA 800
CAL-COMP

Fig. 1 Diagram showing how meteorologic data were collated and handled.

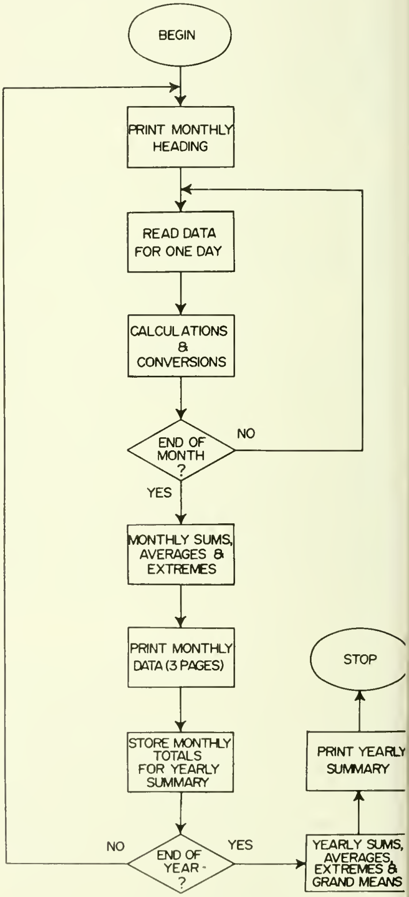

BEGIN
PRINT MONTHLY HEADING
READ DATA FOR ONE DAY
CALCULATIONS & CONVERSIONS
END OF MONTH ?
NO
YES
MONTHLY SUMS, AVERAGES & EXTREMES
PRINT MONTHLY DATA (3 PAGES)
STORE MONTHLY TOTALS FOR YEARLY SUMMARY
END OF YEAR ?
NO
YES
YEARLY SUMS, AVERAGES, EXTREMES & GRAND MEANS
PRINT YEARLY SUMMARY
STOP

Fig. 2. Flow chart for the data tabulation program.

plotting of 10 different meteorologic measurements and 3 calculated mean temperature comparisons. Each deck of program data for any one year must be preceded by a control card identifying the year and number of days in that year. Also included on the control card for the Calcomp plotting program is a list of identifying numbers which permit selection of desired graphs for that year. These graphs are then completed sequentially as selected.

Figures 6 through 18 depict computerized reproduction of 10 different meterologic measurements taken during 1973 and 3 calculated comparisons of means as indicated on each individual legend. Table 6 gives information for the 1973 data regarding the approximate run times and current costs for the IBM 360/65 installation at Brigham Young University.

The complete printout of all daily, monthly, and yearly data is available upon request for the cost of reproduction. Both computer programs are printed herein (Appendix) for researchers who might find sections or subroutines applicable to their specific needs in meteorology or biology.

Regarding specific handling of meteoro-

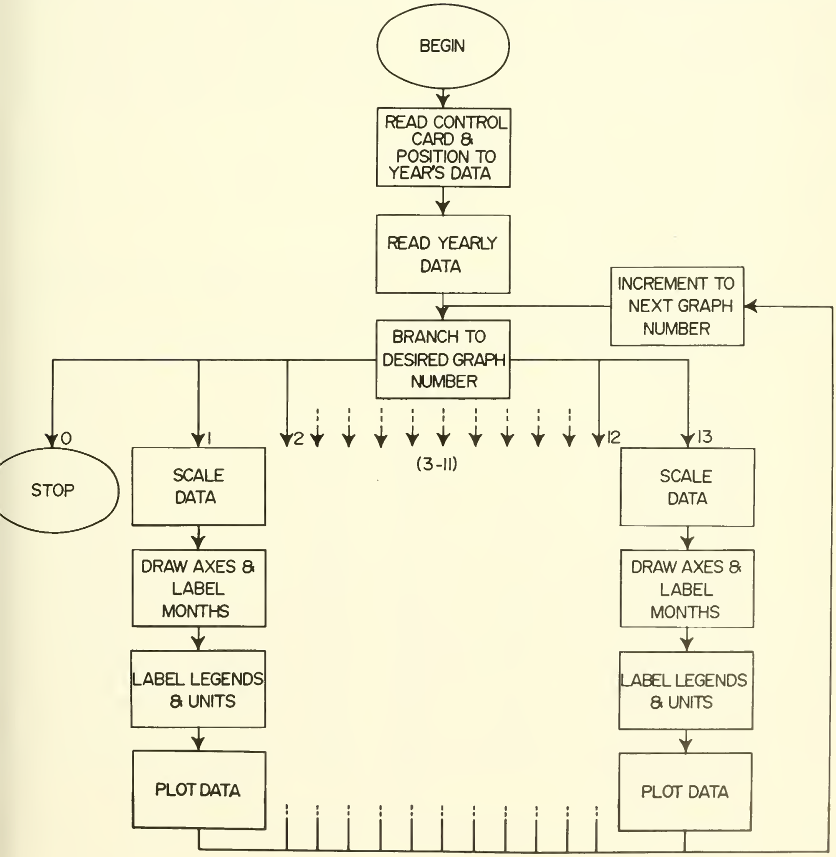

BEGIN
READ CONTROL CARD & POSITION TO YEAR'S DATA
READ YEARLY DATA
INCREMENT TO NEXT GRAPH NUMBER
BRANCH TO DESIRED GRAPH NUMBER
0
1
2
12
13
(3-II)
STOP
SCALE DATA
DRAW AXES & LABEL MONTHS
LABEL LEGENDS & UNITS
PLOT DATA
SCALE DATA
DRAW AXES & LABEL MONTHS
LABEL LEGENDS & UNITS
PLOT DATA

Fig. 3. Flow chart for the Calcomp plotting program.

TABLE 1. Sample monthly summary of measurements on precipitation, soil moisture, relative humidity, potential evaporation, cloud cover, and wind—May 1973.

		PRECIPITATION (MM)					SOIL MOISTURE					RELATIVE HUMIDITY					
DAY	DAY OF YEAR	TOTAL PREC	RAIN PREC	SNOW PREC	SNOW FALL	SNOW COVER	IRRIGATED PERCENT	DEW	IRR*	NON-IRRIG PERCENT	DEW	MAX	MIN	HRS OF 98-100 REL-HUM	POT EVAP (MM)	CLOUD COVER (0-10)	WIND (KM)
1	121	1.0	1.0					+			+	100	68	18	0.0	5	50
2	122	0.3	0.3									100	24	6	7.0	1	34
3	123							+			+	100	30	2	8.2	5	50
4	124											86	38	0	4.8	5	61
5	125							+			+	100	37	11	2.8	8	50
6	126	0.5	0.5					+			+	100	72	8	8.8	4	66
7	127						12.6	+	+	9.2	+	98	42	4	7.2	5	42
8	128						17.5					100	46	9	10.4	9	56
9	129							+			+	98	26	5	8.6	0	29
10	130							+			+	99	40	6	7.4	1	34
11	131							+			+	98	32	8	9.0	0	24
12	132							+			+	98	34	4	10.0	2	32
13	133							+			+	58	30	0	10.0	0	63
14	134						9.9	+	+	8.9	+	100	32	4	8.4	1	61
15	135						20.7					100	36	6	8.6	0	34
16	136							+			+	100	34	4	13.4	0	37
17	137											100	36	5	10.0	1	37
18	138											100	36	5	10.0	0	42
19	139	2.5	2.5					+			+	100	43	8	11.6	0	61
20	140	0.5	0.5					+			+	100	41	8	6.8	3	55
21	141						8.1	+	+	4.4	+	100	38	6	2.0	7	58
22	142						18.9	+			+	100	38	6	7.6	0	31
23	143							+			+	100	32	1	10.2	0	35
24	144	5.1	5.1									100	36	4	5.2	4	82
25	145	24.1	24.1					+			+	100	82	22	0.2	10	39
26	146											99	44	12	6.6	8	82
27	147							+			+	99	36	8	9.6	0	60
28	148						16.8	+	+	15.3	+	100	35	9	8.8	0	21
29	149						24.1	+			+	100	28	4	9.2	0	34
30	150							+				100	36	7	8.6	0	18
31	151							+				100	38	6	9.2	2	40
TOTALS		34.0	34.0	0.0	0.0	0.0	128.6	23	4	37.7	21				240.2		1418
MEANS		1.1	1.1	0.0	0.0	0.0	16.1			9.4		97	39	6	7.7	2	45
EXTREMES																	
HIGH		24.1	24.1	0.0	0.0	0.0	24.1			15.3		100	82	22	13.4	10	82
LOW		0.0	0.0	0.0	0.0	0.0	8.1			4.4		58	24	0	0.0	0	18

* DATE OF IRRIGATION (MAY THROUGH OCTOBER)

TABLE 2. Sample monthly summary of temperatures measured from a standard weather shelter and at 5 cm beneath soil surface under grass cover—May 1973.

		WEATHER SHELTER TEMPERATURES						5 CM BENEATH SOIL SURFACE					
		THERMOMETER			HYGROTHERMOGRAPH			IRRIGATED			NON-IRRIGATED		
DAY	DAY OF YEAR	MAX.	MIN.	MEAN	MAX.	MIN.	MEAN	MAX.	MIN.	MEAN	MAX.	MIN.	MEAN
1	121	13.3	-3.3	5.0	8.9	-1.1	3.9	12.0	6.0	9.0	12.0	6.0	9.0
2	122	15.6	0.0	7.8	15.0	0.0	7.5	16.0	8.0	12.0	17.0	7.0	12.0
3	123	21.7	6.7	14.2	21.1	7.8	14.4	19.0	11.0	15.0	30.0	11.0	20.5
4	124	21.1	7.8	14.4	20.6	7.8	14.2	18.0	12.0	15.0	20.0	12.0	16.0
5	125	20.0	5.0	12.5	19.4	5.6	12.5	18.0	11.0	14.5	18.0	11.0	14.5
6	126	18.9	6.7	12.8	18.3	7.8	13.1	18.0	12.0	15.0	20.0	12.0	16.0
7	127	18.9	6.1	12.5	6.1	6.7	6.4	19.0	13.0	16.0	21.0	13.0	17.0
8	128	19.4	2.2	10.8	18.3	2.2	10.3	17.0	10.0	13.5	19.0	10.0	14.5
9	129	23.9	5.0	14.4	23.3	5.6	14.4	20.0	12.0	16.0	23.0	12.0	17.5
10	130	23.3	4.4	13.9	22.2	4.4	13.3	21.0	12.0	16.5	24.0	13.0	18.5
11	131	23.9	6.1	15.0	22.8	5.6	14.2	20.0	10.0	15.0	21.0	11.0	16.0
12	132	26.7	8.3	17.5	25.6	6.7	16.1	23.0	11.0	17.0	23.0	12.0	17.5
13	133	26.1	8.3	17.2	25.6	8.3	16.9	23.0	12.0	17.5	24.0	13.0	18.5
14	134	25.6	6.1	15.8	24.4	6.7	15.6	23.0	10.0	16.5	24.0	12.0	18.0
15	135	25.6	5.6	15.6	25.6	6.1	15.8	25.0	11.0	18.0	24.0	11.0	17.5
16	136	27.8	6.7	17.2	26.7	7.2	16.9	25.0	12.0	18.5	24.0	13.0	18.5
17	137	28.3	7.2	17.8	27.8	7.8	17.8	26.0	13.0	19.5	26.0	13.0	19.5
18	138	30.0	10.0	20.0	28.9	11.1	20.0	24.0	15.0	19.5	27.0	16.0	21.5
19	139	27.8	10.0	18.9	27.2	10.6	18.9	26.0	14.0	20.0	26.0	14.0	20.0
20	140	26.1	10.6	18.3	25.0	11.1	18.1	26.0	15.0	20.5	25.0	15.0	20.0
21	141	23.3	5.0	14.2	21.7	5.6	13.6	25.0	12.0	18.5	26.0	13.0	19.5
22	142	23.9	5.0	14.4	23.3	5.6	14.4	25.0	12.0	18.5	27.0	14.0	20.5
23	143	26.7	10.6	18.6	26.1	11.1	18.6	27.0	15.0	21.0	28.0	16.0	22.0
24	144	27.2	9.4	18.3	26.7	10.0	18.3	25.0	15.0	20.0	27.0	16.0	21.5
25	145	12.2	3.9	8.1	10.0	4.4	7.2	15.0	10.0	12.5	16.0	10.0	13.0
26	146	13.9	0.0	6.9	13.3	1.1	7.2	19.0	9.0	14.0	20.0	10.0	15.0
27	147	17.2	1.7	9.4	15.6	2.2	8.9	20.0	10.0	15.0	22.0	11.0	16.5
28	148	22.2	3.9	13.1	21.1	4.4	12.8	23.0	12.0	17.5	35.0	12.0	23.5
29	149	23.9	6.1	15.0	23.3	6.7	15.0	24.0	12.0	18.0	26.0	13.0	19.5
30	150	25.0	6.7	15.8	24.4	6.7	15.6	24.0	14.0	19.0	27.0	15.0	21.0
31	151	26.1	9.4	17.8	25.6	10.0	17.8	22.0	15.0	18.5	25.0	16.0	20.5
MEANS		22.8	5.8	14.3	21.4	6.3	13.9	21.5	11.8	16.7	23.5	12.4	17.9
EXTREMES													
HIGH		30.0	10.6		28.9	11.1		27.0	15.0		35.0	16.0	
LOW		12.2	-3.3		6.1	-1.1		12.0	6.0		12.0	6.0	

ALL TEMPERATURES IN DEGREES CELSIUS

Table 3. Sample monthly summary of temperatures measured from a standard weather shelter, at soil surface under grass cover, and on bare soil surface—May 1973.

		WEATHER SHELTER			SOIL SURFACE UNDER GRASS COVER						BARE SOIL SURFACE					
		THERMOMETER			IRRIGATED			NON-IRRIGATED			IRRIGATED			NON-IRRIGATED		
DAY	DAY OF YEAR	MAX.	MIN.	MEAN	MAX.	MIN.	MEAN	MAX.	MIN.	MEAN	MAX.	MIN.	MEAN	MAX.	MIN.	MEAN
1	121	13.3	-3.3	5.0	18.0	4.0	11.0	18.0	3.0	10.5	29.0	-1.0	14.0	32.0	0.0	16.0
2	122	15.6	0.0	7.8	20.0	6.0	13.0	24.0	5.0	14.5	36.0	0.0	18.0	37.0	1.0	19.0
3	123	21.7	6.7	14.2	23.0	9.0	16.0	32.0	9.0	20.5	43.0	5.0	24.0	44.0	7.0	25.5
4	124	21.1	7.8	14.4	26.0	10.0	18.0	17.0	10.0	13.5	45.0	6.0	25.5	47.0	8.0	27.5
5	125	20.0	5.0	12.5	21.0	9.0	15.0	24.0	9.0	16.5	41.0	5.0	23.0	42.0	6.0	24.0
6	126	18.9	6.7	12.8	22.0	11.0	16.5	24.0	11.0	17.5	42.0	6.0	24.0	45.0	7.0	26.0
7	127	18.9	6.1	12.5	24.0	11.0	17.5	26.0	12.0	19.0	47.0	6.0	26.5	52.0	8.0	30.0
8	128	19.4	2.2	10.8	20.0	8.0	14.0	22.0	8.0	15.0	38.0	2.0	20.0	42.0	4.0	23.0
9	129	23.9	5.0	14.4	25.0	10.0	17.5	28.0	10.0	19.0	50.0	-1.0	24.5	55.0	6.0	30.5
10	130	23.3	4.4	13.9	25.0	10.0	17.5	30.0	10.0	20.0	52.0	3.0	27.5	55.0	0.0	27.5
11	131	23.9	6.1	15.0	32.0	10.0	21.0	30.0	8.0	19.0	39.0	8.0	23.5	39.0	4.0	21.5
12	132	26.7	8.3	17.5	38.0	10.0	24.0	35.0	9.0	22.0	50.0	8.0	29.0	51.0	4.0	27.5
13	133	26.1	8.3	17.2	37.0	11.0	24.0	35.0	9.0	22.0	52.0	9.0	30.5	52.0	0.0	26.0
14	134	25.6	6.1	15.8	42.0	10.0	26.0	36.0	8.0	22.0	54.0	8.0	31.0	55.0	4.0	29.5
15	135	25.6	5.6	15.6	40.0	10.0	25.0	35.0	8.0	21.5	55.0	7.0	31.0	57.0	2.0	29.5
16	136	27.8	6.7	17.2	43.0	11.0	27.0	36.0	9.0	22.5	56.0	9.0	32.5	58.0	4.0	31.0
17	137	28.3	7.2	17.8	43.0	12.0	27.5	39.0	10.0	24.5	59.0	10.0	34.5	58.0	5.0	31.5
18	138	30.0	10.0	20.0	42.0	15.0	28.5	41.0	16.0	28.5	60.0	15.0	37.5	59.0	10.0	34.5
19	139	27.8	10.0	18.9	49.0	14.0	31.5	43.0	12.0	27.5	61.0	12.0	36.5	61.0	8.0	34.5
20	140	26.1	10.6	18.3	46.0	14.0	30.0	37.0	13.0	25.0	52.0	13.0	32.5	53.0	8.0	30.5
21	141	23.3	5.0	14.2	36.0	12.0	24.0	38.0	9.0	23.5	32.0	9.0	20.5	53.0	4.0	28.5
22	142	23.9	5.0	14.4	44.0	9.0	26.5	43.0	9.0	26.0	45.0	9.0	27.0	57.0	4.0	30.5
23	143	26.7	10.6	18.6	45.0	13.0	29.0	40.0	13.0	26.5	50.0	14.0	32.0	60.0	10.0	35.0
24	144	27.2	9.4	18.3	47.0	14.0	30.5	45.0	14.0	29.5	52.0	9.0	30.5	59.0	11.0	35.0
25	145	12.2	3.9	8.1	18.0	4.0	11.0	17.0	7.0	12.0	17.0	7.0	12.0	15.0	3.0	9.0
26	146	13.9	0.0	6.9	34.0	8.0	21.0	27.0	7.0	17.0	31.0	6.0	18.5	28.0	2.0	15.0
27	147	17.2	1.7	9.4	36.0	8.0	22.0	31.0	8.0	19.5	37.0	6.0	21.5	38.0	5.0	21.5
28	148	22.2	3.9	13.1	32.0	11.0	21.5	36.0	10.0	23.0	34.0	9.0	21.5	47.0	7.0	27.0
29	149	23.9	6.1	15.0	40.0	11.0	25.5	39.0	10.0	24.5	38.0	9.0	23.5	51.0	8.0	29.5
30	150	25.0	6.7	15.8	39.0	12.0	25.5	39.0	12.0	25.5	43.0	11.0	27.0	52.0	10.0	31.0
31	151	26.1	9.4	17.8	39.0	14.0	26.5	38.0	14.0	26.0	46.0	14.0	30.0	53.0	12.0	32.5
MEANS		22.8	5.8	14.3	33.7	10.4	22.0	32.4	9.7	21.1	44.7	7.5	26.1	48.6	5.5	27.1
EXTREMES																
HIGH		30.0	10.6		49.0	15.0		45.0	16.0		61.0	15.0		61.0	12.0	
LOW		12.2	-3.3		18.0	4.0		17.0	3.0		17.0	-1.0		15.0	0.0	

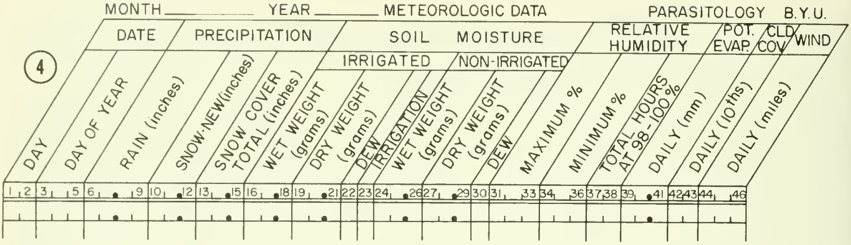
ALL TEMPERATURES IN DEGREES CELSIUS

Table 4. Yearly summary of measurements on precipitation, soil moisture, relative humidity, potential evaporation, cloud cover, and wind—1973.

		PRECIPITATION (MM)					SOIL MOISTURE (PERCENT)		RELATIVE HUMIDITY					
MONTH		TOTAL PREC	RAIN PREC	SNOW PREC	SNOW FALL	SNOW COVER	IRRG	NON-IRRG	MAX	MIN	HRS OF 98-100 REL HUM	POT EVAP (MM)	CLOUD COVER (0-10)	WIND (KM)
JANUARY	TOTAL	29.7	0.0	29.7	297.2	3302.0	--	--	--	--	--	ND	--	1183
	MEAN	1.0	0.0	1.0	9.6	106.5	ND	ND	98	76	17	ND	6	38
FEBRUARY	TOTAL	33.8	31.7	2.0	20.3	363.2	--	--	--	--	--	ND	--	1144
	MEAN	1.2	1.1	0.1	0.7	13.0	ND	ND	98	66	14	ND	5	40
MARCH	TOTAL	86.6	58.7	27.9	279.4	287.0	--	--	--	--	--	ND	--	2012
	MEAN	2.8	1.9	0.9	9.0	9.3	ND	ND	98	57	11	ND	6	64
APRIL	TOTAL	44.4	33.0	11.4	114.3	114.3	--	--	--	--	--	ND	--	1901
	MEAN	1.5	1.1	0.4	3.8	3.8	ND	ND	98	50	8	ND	4	63
MAY	TOTAL	34.0	34.0	0.0	0.0	0.0	--	--	--	--	--	240.2	--	1418
	MEAN	1.1	1.1	0.0	0.0	0.0	16.1	9.4	97	39	6	7.7	2	45
JUNE	TOTAL	18.3	18.3	0.0	0.0	0.0	--	--	--	--	--	268.6	--	1215
	MEAN	0.6	0.6	0.0	0.0	0.0	20.6	8.9	97	35	5	9.0	2	40
JULY	TOTAL	19.8	19.8	0.0	0.0	0.0	--	--	--	--	--	299.0	--	889
	MEAN	0.6	0.6	0.0	0.0	0.0	16.7	4.0	99	39	7	9.6	1	28
AUGUST	TOTAL	51.8	51.8	0.0	0.0	0.0	--	--	--	--	--	368.4	--	1061
	MEAN	1.7	1.7	0.0	0.0	0.0	31.2	11.7	98	34	7	11.9	1	34
SEPTEMBER	TOTAL	39.4	39.4	0.0	0.0	0.0	--	--	--	--	--	197.8	--	766
	MEAN	1.3	1.3	0.0	0.0	0.0	26.1	12.4	99	46	9	6.6	2	25
OCTOBER	TOTAL	13.2	13.2	0.0	0.0	0.0	--	--	--	--	--	88.4	--	1198
	MEAN	0.4	0.4	0.0	0.0	0.0	25.7	10.1	99	42	8	2.9	2	38
NOVEMBER	TOTAL	80.5	17.0	63.5	635.0	1531.6	--	--	--	--	--	ND	--	1210
	MEAN	2.7	0.6	2.1	21.2	51.1	ND	ND	99	58	11	ND	5	40
DECEMBER	TOTAL	45.0	0.0	45.0	449.6	970.3	--	--	--	--	--	ND	--	1329
	MEAN	1.5	0.0	1.5	14.5	31.3	ND	ND	99	69	15	ND	5	42
YEARLY TOTAL		496.6	317.0	179.6	1795.8	6568.4	--	--	--	--	--	1462.4*	--	15326
GRAND MEAN		1.4	0.9	0.5	4.9	17.9	22.7*	9.4*	98	50	9	7.9*	3	41

ND = NOT DETERMINED
* CALCULATED 1 MAY THROUGH 31 OCTOBER ONLY

④


MONTH
YEAR
METEOROLOGIC DATA
PARASITOLOGY B.Y.U.
DATE
PRECIPITATION
SOIL MOISTURE
IRRIGATED
NON-IRRIGATED
RELATIVE HUMIDITY
POT. EVAP.
CLD. COV.
WIND
DAY
DAY OF YEAR
RAIN (inches)
SNOW-NEW (inches)
SNOW COVER TOTAL (inches)
WET WEIGHT (grams)
DRY WEIGHT (grams)
DEW
IRRIGATION
WET WEIGHT (grams)
DRY WEIGHT (grams)
DEW
MAXIMUM %
MINIMUM %
TOTAL HOURS AT 98-100%
DAILY (mm)
DAILY (10ths)
DAILY (miles)

⑤

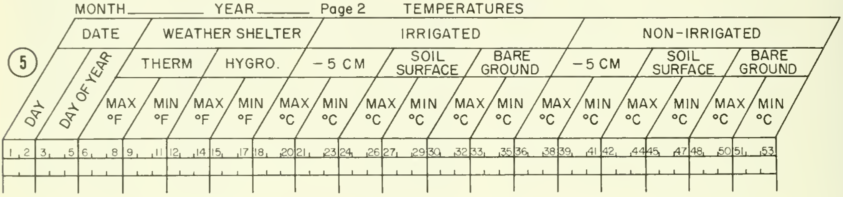

MONTH
YEAR
Page 2
TEMPERATURES
DATE
WEATHER SHELTER
IRRIGATED
NON-IRRIGATED
THERM
HYGRO.
−5 CM
SOIL SURFACE
BARE GROUND
−5 CM
SOIL SURFACE
BARE GROUND
DAY
DAY OF YEAR
MAX °F
MIN °F
MAX °F
MIN °F
MAX °C
MIN °C
MAX °C
MIN °C
MAX °C
MIN °C
MAX °C
MIN °C
MAX °C
MIN °C
MAX °C
MIN °C

TABLE 5. Yearly summary of temperatures measured in a standard weather shelter, at 5 cm beneath soil surface under grass cover, at soil surface under grass cover, and on bare soil surface—1973.

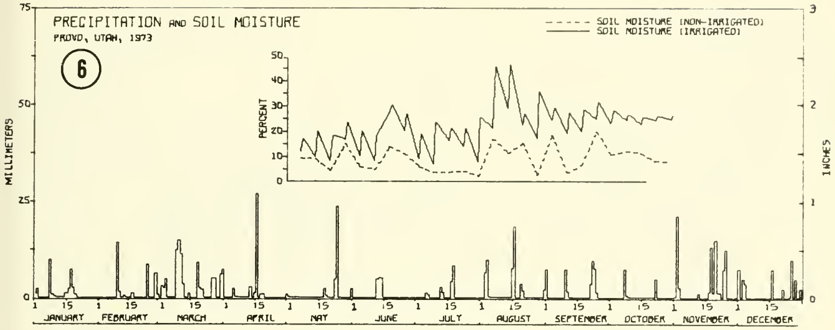
	WEATHER SHELTER TEMPERATURES						5 CM BENEATH SOIL SURFACE					
	THERMOMETER			HYGROTHERMOGRAPH			IRRIGATED			NON-IRRIGATED		
MONTH	MAX.	MIN.	MEAN	MAX.	MIN.	MEAN	MAX.	MIN.	MEAN	MAX.	MIN.	MEAN
JANUARY	0.6	-12.6	-6.0	-1.1	-11.4	-6.2	-3.4	-4.2	-3.8	-2.4	-3.4	-2.9
FEBRUARY	6.6	-6.3	0.2	5.1	-5.9	-0.4	-1.8	-3.5	-2.7	-0.9	-2.4	-1.6
MARCH	9.0	-3.2	2.9	7.7	-2.5	2.6	4.0	-1.2	1.4	6.1	0.2	3.1
APRIL	12.9	-0.7	6.1	11.6	0.1	5.8	8.4	1.9	5.1	10.5	3.2	6.9
MAY	22.8	5.8	14.3	21.4	6.3	13.9	21.5	11.8	16.7	23.5	12.4	17.9
JUNE	27.4	8.9	18.2	26.7	9.5	18.1	24.7	15.2	19.9	29.7	16.6	23.1
JULY	31.0	12.4	21.7	30.8	13.3	22.0	28.1	19.1	23.6	34.5	20.2	27.4
AUGUST	31.5	11.8	21.6	31.0	12.8	21.9	26.5	18.4	22.5	31.9	18.8	25.4
SEPTEMBER	23.3	5.5	14.4	22.9	6.7	14.8	19.1	12.6	15.8	22.6	12.1	17.4
OCTOBER	19.4	2.1	10.7	19.0	3.2	11.1	13.0	7.9	10.5	16.2	7.5	11.9
NOVEMBER	9.9	-2.2	3.9	9.3	-1.2	4.0	4.7	2.5	3.6	5.4	2.2	3.8
DECEMBER	5.2	-5.6	-0.2	4.9	-4.7	0.1	0.7	-0.7	-0.0	0.4	-1.1	-0.4
GRAND MEAN	16.6	1.3	9.0	15.8	2.2	9.0	12.1	6.6	9.4	14.8	7.2	11.0

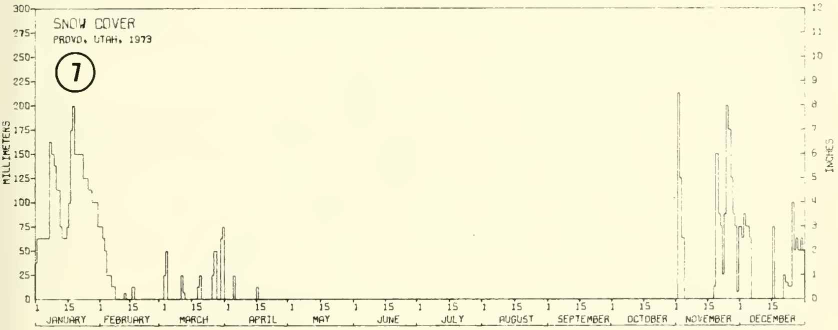
	SOIL SURFACE UNDER GRASS COVER						BARE SOIL SURFACE					
	IRRIGATED			NON-IRRIGATED			IRRIGATED			NON-IRRIGATED		
MONTH	MAX.	MIN.	MEAN	MAX.	MIN.	MEAN	MAX.	MIN.	MEAN	MAX.	MIN.	MEAN
JANUARY	-1.9	-2.5	-2.2	-2.7	-4.2	-3.4	-3.1	-4.5	-3.8	-2.8	-3.9	-3.4
FEBRUARY	1.0	-2.4	-0.7	2.0	-2.9	-0.5	6.5	-5.6	0.4	5.8	-4.3	0.8
MARCH	7.9	-0.3	3.8	10.0	-1.0	4.5	17.5	-4.4	6.5	18.6	-3.1	7.8
APRIL	12.4	2.6	7.5	15.7	2.1	8.9	25.1	-2.4	11.3	29.3	-1.0	14.1
MAY	33.7	10.4	22.0	32.4	9.7	21.1	44.7	7.5	26.1	48.6	5.5	27.1
JUNE	41.2	13.4	27.3	43.1	13.3	28.2	46.2	12.7	29.4	57.5	10.3	33.9
JULY	35.7	19.8	27.8	50.9	16.4	33.6	44.9	16.3	30.6	62.8	14.5	38.7
AUGUST	32.6	19.5	26.0	44.3	15.9	30.1	44.0	15.8	29.9	55.5	14.2	34.9
SEPTEMBER	24.8	13.4	19.1	31.3	9.7	20.5	33.3	10.1	21.7	40.6	8.0	24.3
OCTOBER	18.0	9.0	13.5	22.8	5.1	14.0	25.1	6.4	15.7	32.8	2.4	17.6
NOVEMBER	8.0	4.3	6.2	7.8	1.2	4.5	12.6	1.8	7.2	12.6	0.0	6.3
DECEMBER	3.5	1.3	2.4	1.8	-1.2	0.3	6.3	-0.4	3.0	4.1	-2.1	1.0
GRAND MEAN	18.1	7.4	12.7	21.6	5.3	13.5	25.3	4.4	14.8	30.5	3.4	16.9

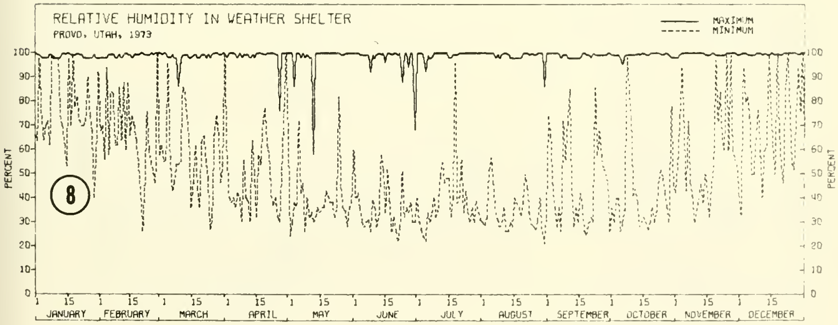
ALL TEMPERATURES IN DEGREES CELSIUS

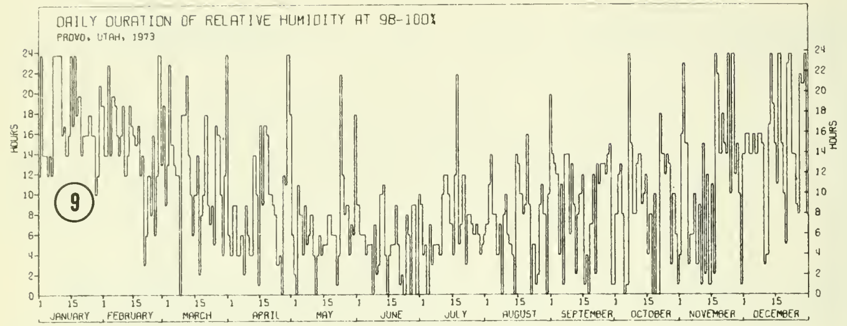
Table 6. 1973 data for time and costs for weather data tabulation and Calcomp plotting programs using the IBM 360/65 installation at Brigham Young University.

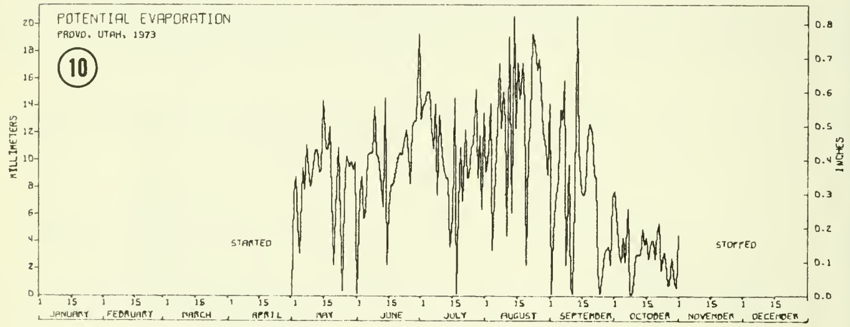
Program	Turn around time	Compiler costs	Run costs	Plotter costs	Total
Weather data tabulation	0.5 hr	$6.75	$ 7.50	--	$14.25
Calcomp graphics	2.0 hr	$7.00	$13.00	$5.00	$25.00
					$39.25

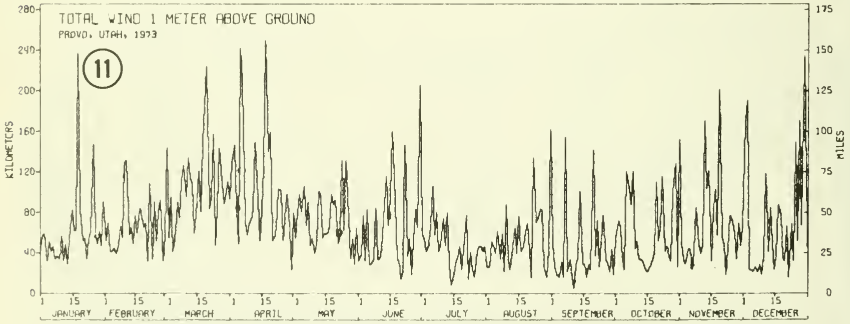

PRECIPITATION AND SOIL MOISTURE
PROVO, UTAH, 1973
6
SOIL MOISTURE (NON-IRRIGATED)
SOIL MOISTURE (IRRIGATED)
MILLIMETERS
0
25
50
75
INCHES
0
1
2
3
PERCENT
0
10
20
30
40
50
1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15
JANUARY FEBRUARY MARCH APRIL MAY JUNE JULY AUGUST SEPTEMBER OCTOBER NOVEMBER DECEMBER

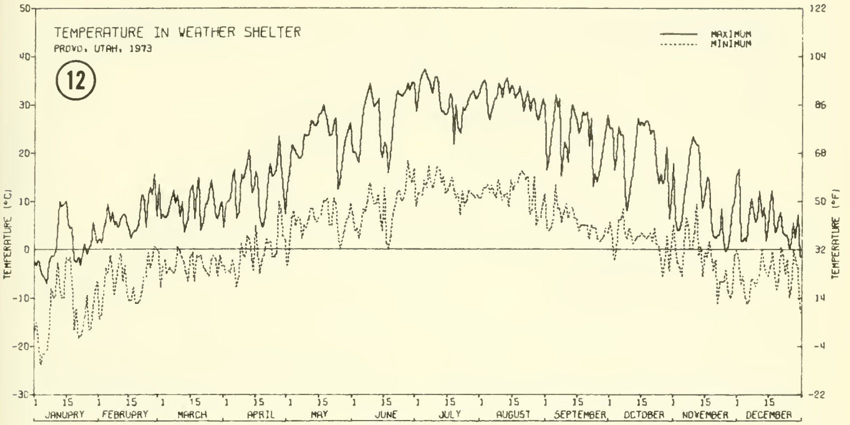

SNOW COVER
PROVO, UTAH, 1973
7
MILLIMETERS
0
25
50
75
100
125
150
175
200
225
250
275
300
INCHES
0
1
2
3
4
5
6
7
8
9
10
11
12
1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15
JANUARY FEBRUARY MARCH APRIL MAY JUNE JULY AUGUST SEPTEMBER OCTOBER NOVEMBER DECEMBER

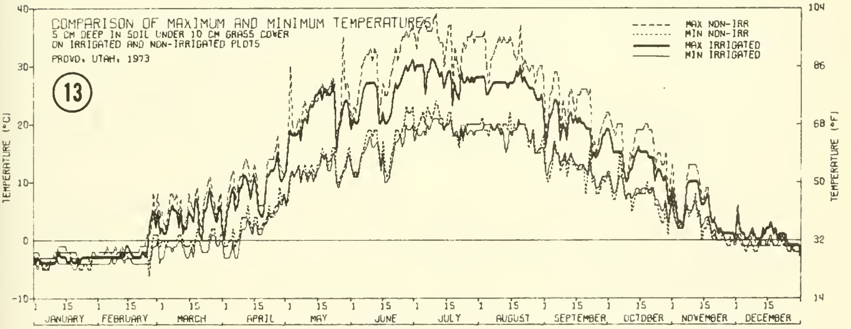

RELATIVE HUMIDITY IN WEATHER SHELTER
PROVO, UTAH, 1973
MAXIMUM
MINIMUM
8
PERCENT
0
10
20
30
40
50
60
70
80
90
100
1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15
JANUARY FEBRUARY MARCH APRIL MAY JUNE JULY AUGUST SEPTEMBER OCTOBER NOVEMBER DECEMBER

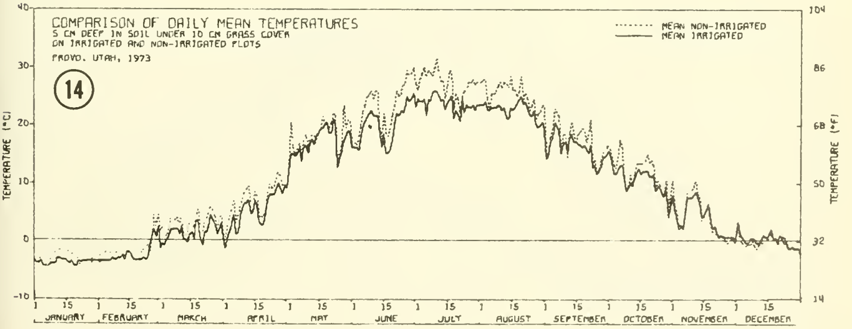

DAILY DURATION OF RELATIVE HUMIDITY AT 98-100%
PROVO, UTAH, 1973
9
HOURS
0
2
4
6
8
10
12
14
16
18
20
22
24
1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER

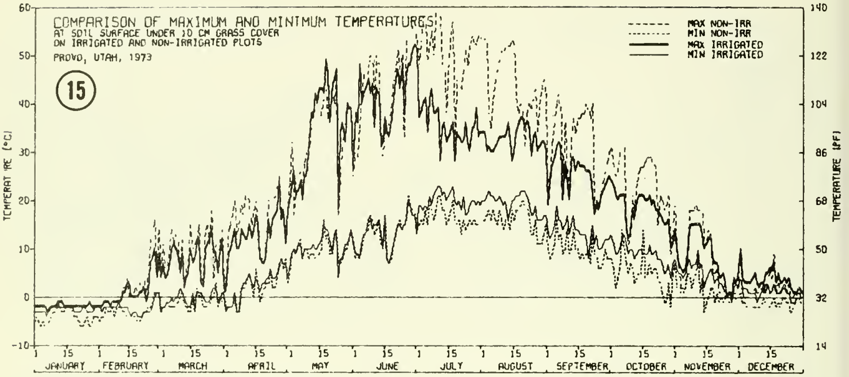

POTENTIAL EVAPORATION
PROVO, UTAH, 1973
10
MILLIMETERS
0
2
4
6
8
10
12
14
16
18
20
INCHES
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
STARTED
STOPPED
1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER

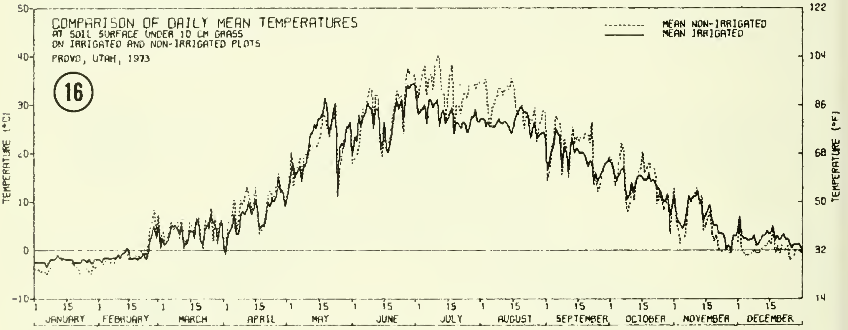

TOTAL WIND 1 METER ABOVE GROUND
PROVO, UTAH, 1973
11
KILOMETERS
0
40
80
120
160
200
240
280
MILES
0
25
50
75
100
125
150
175
1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15 1 15
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER

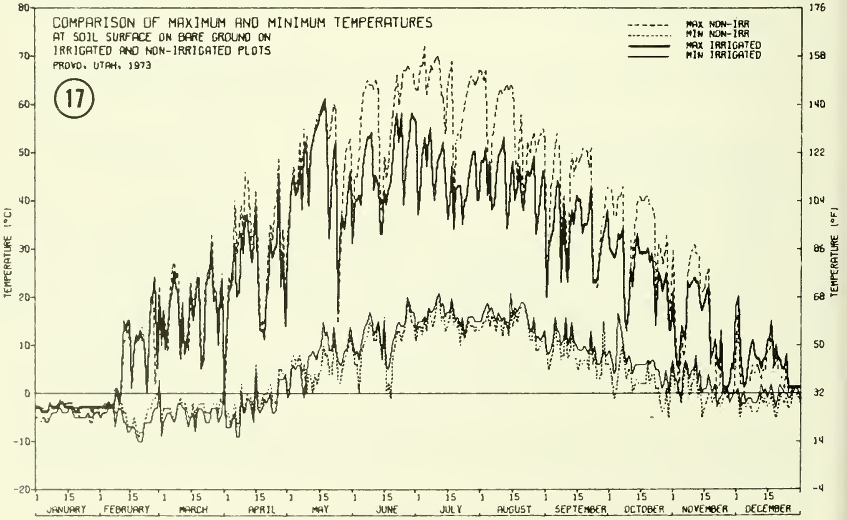

TEMPERATURE IN WEATHER SHELTER
PROVO, UTAH, 1973
12
MAXIMUM
MINIMUM
TEMPERATURE (°C)
TEMPERATURE (°F)
50
40
30
20
10
0
-10
-20
-30
122
104
86
68
50
32
14
-4
-22
1 15
JANUARY FEBRUARY MARCH APRIL MAY JUNE JULY AUGUST SEPTEMBER OCTOBER NOVEMBER DECEMBER

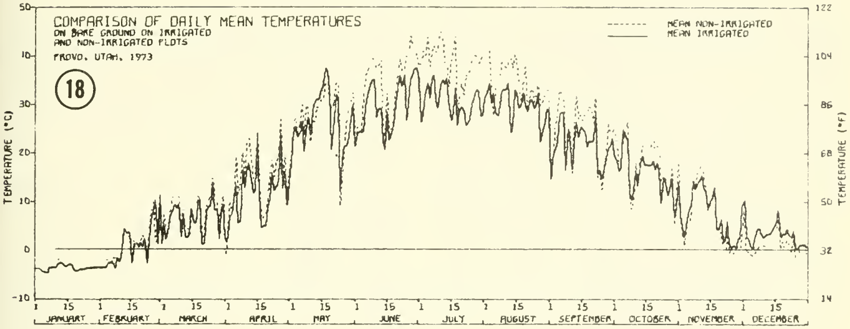

COMPARISON OF MAXIMUM AND MINIMUM TEMPERATURES
5 CM DEEP IN SOIL UNDER 10 CM GRASS COVER
ON IRRIGATED AND NON-IRRIGATED PLOTS
PROVO, UTAH, 1973
13
MAX NON-IRR
MIN NON-IRR
MAX IRRIGATED
MIN IRRIGATED
TEMPERATURE (°C)
TEMPERATURE (°F)
40
30
20
10
0
-10
104
86
68
50
32
14
1 15
JANUARY FEBRUARY MARCH APRIL MAY JUNE JULY AUGUST SEPTEMBER OCTOBER NOVEMBER DECEMBER


COMPARISON OF DAILY MEAN TEMPERATURES
5 CM DEEP IN SOIL UNDER 10 CM GRASS COVER
ON IRRIGATED AND NON-IRRIGATED PLOTS
PROVO, UTAH, 1973
14
MEAN NON-IRRIGATED
MEAN IRRIGATED
TEMPERATURE (°C)
TEMPERATURE (°F)
40
30
20
10
0
-10
104
86
68
50
32
14
1 15
JANUARY FEBRUARY MARCH APRIL MAY JUNE JULY AUGUST SEPTEMBER OCTOBER NOVEMBER DECEMBER


COMPARISON OF MAXIMUM AND MINIMUM TEMPERATURES
AT SOIL SURFACE UNDER 10 CM GRASS COVER
ON IRRIGATED AND NON-IRRIGATED PLOTS
PROVO, UTAH, 1973
15
MAX NON-IRR
MIN NON-IRR
MAX IRRIGATED
MIN IRRIGATED
TEMPERATURE (°C)
TEMPERATURE (°F)
60
50
40
30
20
10
0
-10
140
122
104
86
68
50
32
14
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER


COMPARISON OF DAILY MEAN TEMPERATURES
AT SOIL SURFACE UNDER 10 CM GRASS
ON IRRIGATED AND NON-IRRIGATED PLOTS
PROVO, UTAH, 1973
16
MEAN NON-IRRIGATED
MEAN IRRIGATED
TEMPERATURE (°C)
TEMPERATURE (°F)
50
40
30
20
10
0
-10
122
104
86
68
50
32
14
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER


COMPARISON OF MAXIMUM AND MINIMUM TEMPERATURES
AT SOIL SURFACE ON BARE GROUND ON
IRRIGATED AND NON-IRRIGATED PLOTS
PROVO, UTAH, 1973
17
MAX NON-IRR
MIN NON-IRR
MAX IRRIGATED
MIN IRRIGATED
TEMPERATURE (°C)
TEMPERATURE (°F)
80
70
60
50
40
30
20
10
0
-10
-20
176
158
140
122
104
86
68
50
32
14
-4
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER



logic information from the pasture plots as well as certain calculations and conversions by the computer, the following clarifications may be warranted. All measurements of precipitation as rain are measured and entered in fractions of inches and then converted before tabulation into millimeter units. New snow and total snow cover are similarly handled. Precipitation as snow is calculated as one-tenth that of total snowfall for any one day. Soil moisture samples were determined as described previously by Andersen et al. (1974), with the exception that two samples were taken each week from the irrigated plot—one just prior to sprinkling of the plot and the second 24 hr later. Only one weekly sample was taken from the nonirrigated plot. The weight in grams of each sample was entered as an original wet weight and then as a dry weight determined after 24 hr storage at 105 C.

Programmed formulae calculated the percent soil moisture by dividing the difference in the wet and dry weight for each sample by the dry weight value. This percent was then printed on the first printout page for each of the six months that irrigation was used. The presence or absence of dew on each plot was noted for each morning during those six months and recorded as a "+" when present. Irrigation by sprinkling was performed each Monday during the six-month period and also indicated with a "+" on the appropriate dates.

Relative humidity (RH) maxima and minima, as well as the total number of hours each day at which 98-100 percent RH occurred, were entered and printed out directly. The evaporating pan on the instrument that measured potential evaporation was filled each morning, and the daily water loss noted for the following 24 hr was entered in mm and also printed out directly. Since evaporation could not be read in freezing weather, the measurement was taken only during May through October, those same months during which the one plot was irrigated. A difficulty ensued whenever rain occurred because the evaporating pan held only 20 mm of water and refilled partially or completely on any day during which rain fell. Thus, any potential evaporation which may have occurred on such days was invariably negated to some degree by the rain that collected in the evaporating pan. Nevertheless, the recording evaporimeter used in the study gave a much more accurate reflection of the potential evaporation with its shallow pan (20 mm) than do the large evaporation tanks used by the U.S. Weather Bureau. In those tanks the water level is frequently 4-6 in (10-15 cm) below the upper rim of the pan and hence protected markedly from the evaporating effect of wind currents.

Any evaluation of daily cloud cover was determined visually each morning and recorded in tenths. The evaluation indicated the approximate portion of the sky that was covered sufficiently with clouds to cast a shadow at the time the instruments were read. It was thus the most subjective of all measurements taken but, nevertheless, provided some estimation of cloud cover in this region. Wind totals were entered in mile units read from the anemometer dial each day, calculated as the difference from the value of the preceding day, and converted and printed out as kilometers. The final daily wind total for any preceding year is listed as a starting value and included on the control card for the main program.

Maximum and minimum temperatures monitored from a standard weather shelter, from 5 cm beneath soil surface under grass cover, from soil surface under grass cover, or from bare ground were recorded, converted to Celsius if not already in those units, and printed onto the second and third sheets for each month's data. Means and extremes for all values were stored for eventual calculation of totals and grand means for the annual summary pages.

Daily maximum and minimum temperatures were measured in the weather shelter by mercury- and alcohol-filled thermometers as well as by a standard hygrothermograph. Differences noted in the recorded temperatures relate mainly to the longer time lag required by the bimetallic sensor within the thermograph unit.

Discussion

The main objective of this paper was to present the computer programs developed for our research on the effect of irrigation on pasture microenvironments. These programs have proved extremely satisfactory to us, and hopefully some sections or subroutines will be of value to others engaged in related research projects. Mitchell and Andersen (1969) reported on a computer program, developed at the University of Illinois at Urbana, for handling meteorologic data collected from grass plots. Certain similarities exist between that program and the one reported here, since the choice of meteorologic instruments and the overall research projects at the two institutions were closely correlated. The program at Illinois, however, was designed to handle some additional measurements not taken in the current study, such as solar radiation. The Illinois study also gave emphasis to conversion data for a series of soil-moisture and soil-temperature measurements obtained through moisture-cell leads (wafers) and built-in thermistor units. The programs developed at BYU use data on soil moisture only from simplified gravimetric measurements but include the techniques designed for Calcomp graphing as well. The advantage of this plotting program is not only in the funds saved through not having to manually plot, trace, and label all such graphs but more particularly in the marked reduction of errors that invariably accompany the tedious and laborious tasks encountered in manually plotting daily weather data.

The impact of irrigation on the moisture and temperature profiles in central Utah during 1973 was essentially the same as that reported for 1970-72 by Andersen et al. (1974). Grand mean temperatures for 5 cm beneath soil surface under grass cover, at soil surface under grass cover, or on bare soil surface were consistently lower on the irrigated plot than on the nonirrigated area. These temperature differences were most apparent during the warm summer months when irrigation is commonly employed throughout the region. In July, for example, the month during which most yearly maxima were recorded, the average monthly maximum temperatures measured 5 cm beneath soil surface under grass cover on irrigated and nonirrigated plots differed by 6.4 C, by 15.2 C for those measured at soil surface under grass cover, and by 17.9 C on bare ground. During the six months when no irrigation occurred, the differences were not so apparent; hence the grand means for the year do not give an accurate reflection of these temperature ranges for the irrigation season.

The contrast between soil moisture measurements in the two plots was readily apparent for the six months during which soil samples were gravimetrically analyzed for moisture content. The grand mean for the percent soil moisture for that period was 22.7 percent for the samples removed from the irrigated section and 9.4 percent for those from the nonirrigated area.

Other meteorologic measurements which were taken, such as the precipitation pattern for rain or snow, relative humidity, potential evaporation, and wind, were monitored for both sections combined, since the instruments used could not detect differences from microenvironments. The general pattern of these values was similar to that recorded for previous years. The collective data for 1973 emphasize the marked beneficial impact of irrigation in creating favorable microenvironments for living organisms.

APPENDIX

```
C      **********************************************************************
C      *                                                                    *
C      *        WEATHER DATA ANALYSIS, PART I                               *
C      *                                                                    *
C      *        DEVELOPED BY FERRON ANDERSON, BYU                           *
C      *        PROGRAMMED BY PAUL ROSS ROPER, ERI                          *
C      *                                                                    *
C      **********************************************************************
C
        INTEGER  NDAYS, DAY, DYR, DEW1, IRRG, DEW2, HHUM, LHUM, THRS,
      A          CLCV, WIND, OLDW, S2(26,5), MON(12), HOLD, MONTH(13,3)/
      B          'JANU', 'FEBR', 'MARC', 'APRI', 'MAY ', 'JUNE', 'JULY',
      C          'AUGU', 'SEPT', 'OCTO', 'NOVE', 'DECE', 'GRAN', 'ARY ',
      D          'UARY', 'H   ', 'L   ', 3*'    ', 'ST  ', 'EMBE', 'BER ',
      E          'MBER', 'MBER', 'D ME', 8*'    ', 'R   ', 3*'    ', 'AN  '/
        REAL     TPRE, RAIN, PRSN, SNOW, SNCV, MOSI, MOSN, PEVP, IRWW,
      A          IRDW, NIWW, NIDW, T(34,16), S1(26,8), S3(13,24),
      B          PAGE2(34,12), PAGE3(34,15)
        COMMON   NDAYS, DAY(31), DYR(31), TPRE(35), RAIN(35), PRSN(35),
      A          SNOW(35), SNCV(35), MOSI(35), DEW1(32), IRRG(32),
      B          MOSN(35), DEW2(32), HHUM(35), LHUM(35), THRS(35),
      C          PEVP(35), CLCV(35), WIND(35)
        DATA S1,S2,S3 /208*0.0, 130*0, 312*0.0/
C       TAPE ID
        DATA ITAPE /5/
        CENT(X) = (X-32.0)*5.0/9.0
C
C       REWIND ITAPE
C
C       LOOK FOR CORRECT YEAR
C
      1 READ(5,200,END=999) NYEAR
      2 READ(ITAPE,200,END=999) IYEAR, IDAYS, MON, OLDW
        IF(IYEAR.EQ.NYEAR) GO TO 4
        DO 3 I=1,IDAYS
        READ(ITAPE,200,END=999)
      3 CONTINUE
        GO TO 2
C
C
C       PROCESS DATA PAGE BY PAGE
C
      4 DO 900 II=1,12
        CALL HEAD (IYEAR,II,1,MONTH)
        NDAYS = MON(II)
C
C       WRITE PAGE 1 HEADING
C
        WRITE(6,120)
        DO 10 I=1,NDAYS
        READ(ITAPE,201) DAY(I), DYR(I), RAIN(I), SNOW(I), SNCV(I), IRWW,
      A                   IRDW, DEW1(I), IRRG(I), NIWW, NIDW, DEW2(I),
      B                   HHUM(I), LHUM(I), THRS(I), PEVP(I), CLCV(I),
      C                   WIND(I), (T(I,J),J=1,16)
        PRSN(I) = SNOW(I) * 0.1
        TPRE(I) = RAIN(I) + PRSN(I)
        IF(OLDW.GT.WIND(I)) OLDW = OLDW - 1000
        HOLD = WIND(I)
        WIND(I) = (WIND(I) - OLDW) * 1.6093 + 0.5
        OLDW = HOLD
        MOSI(I) = 0.0
        MOSN(I) = 0.0
        IF(IRWW.NE.0.0) MOSI(I) = (IRWW - IRDW) * 100 / IRDW
        IF(NIWW.NE.0.0) MOSN(I) = (NIWW - NIDW) * 100 / NIDW
        CALL PRINTL (I,II)
        PAGE2(I,1)  = CENT(T(I,1))
        PAGE2(I,2)  = CENT(T(I,2))
        PAGE2(I,4)  = CENT(T(I,3))
        PAGE2(I,5)  = CENT(T(I,4))
        PAGE2(I,7)  = T(I,5)
        PAGE2(I,8)  = T(I,6)
        PAGE2(I,10) = T(I,11)
      PAGE2(I,11) = T(I,12)
      PAGE3(I,1)  = PAGE2(I,1)
      PAGE3(I,2)  = PAGE2(I,2)
      PAGE3(I,4)  = T(I,7)
      PAGE3(I,5)  = T(I,8)
      PAGE3(I,7)  = T(I,13)
      PAGE3(I,8)  = T(I,14)
      PAGE3(I,10) = T(I,9)
      PAGE3(I,11) = T(I,10)
      PAGE3(I,13) = T(I,15)
      PAGE3(I,14) = T(I,16)
   10 CONTINUE
C
C
      CALL SUMR (TPRE)
      CALL SUMR (RAIN)
      CALL SUMR (PRSN)
      CALL SUMR (SNOW)
      CALL SUMR (SNCV)
      CALL SUMR (PEVP)
      CALL SUMZ (MOSI)
      CALL SUMZ (MOSN)
      CALL SUMI (HHUM)
      CALL SUMI (LHUM)
      CALL SUMI (THRS)
      CALL SUMI (CLCV)
      CALL SUMI (WIND)
      CALL SUMC (IRRG)
      CALL SUMC (DEW1)
      CALL SUMC (DEW2)
C
C     PAGE 1 OF WEATHER DATA
C
      IF(II.LT.5.OR.II.GT.10) GOTO 20
      WRITE(6,121) TPRE(32), RAIN(32), PRSN(32), SNOW(32), SNCV(32),
     A             MOSI(32), DEW1(32), IRRG(32), MOSN(32), DEW2(32),
     B             PEVP(32), WIND(32)
      WRITE(6,122) (TPRE(I), RAIN(I), PRSN(I), SNOW(I), SNCV(I),
     A              MOSI(I), MOSN(I), HHUM(I), LHUM(I), THRS(I),
     B              PEVP(I), CLCV(I), WIND(I),I=33,35)
      GOTO 30
   20 WRITE(6,123) TPRE(32), RAIN(32), PRSN(32), SNOW(32), SNCV(32),
     A             WIND(32)
      WRITE(6,124) (TPRE(I), RAIN(I), PRSN(I), SNOW(I), SNCV(I),
     A             HHUM(I), LHUM(I), THRS(I), CLCV(I), WIND(I),I=33,35)
C
C
C     PAGE 2 OF WEATHER DATA
C
   30 CALL HEAD (IYEAR,II,2,MONTH)
      CALL CALC (PAGE2,12)
      WRITE(6,130)
      DO 31 I=1,NDAYS
   31 WRITE(6,131) DAY(I), DYR(I), (PAGE2(I,J),J=1,12)
      WRITE(6,132) ((PAGE2(I,J),J=1,12),I=32,34)
C
C     PAGE 3 OF WEATHER DATA
C
      CALL HEAD (IYEAR,II,3,MONTH)
      CALL CALC (PAGE3,15)
      WRITE(6,140)
      DO 40 I=1,NDAYS
   40 WRITE(6,141) DAY(I), DYR(I), (PAGE3(I,J),J=1,15)
      WRITE(6,142) ((PAGE3(I,J),J=1,15),I=32,34)
C
C     STORE DATA FOR YEARLY SUMMARY PAGES
C
      DO 50 J=1,2
      K = II * 2 + J - 2
      S1(K,1) = TPRE(31+J)
      S1(K,2) = RAIN(31+J)
      S1(K,3) = PRSN(31+J)
      S1(K,4) = SNOW(31+J)
      S1(K,5) = SNCV(31+J)
      S1(K,6) = MOSI(31+J)
      S1(K,7) = MOSN(31+J)
      S1(K,8) = PEVP(31+J)
   50 S2(K,5) = WIND(31+J)
      S2(K,1) = HHUM(33)
      S2(K,2) = LHUM(33)
      S2(K,3) = THRS(33)
      S2(K,4) = CLCV(33)
      DO 51 J=1,12
      S3(II,J) = PAGE2(32,J)
   51 S3(II,J+12) = PAGE3(32,J+3)
  900 CONTINUE
C
C
C     YEARLY SUMMARY PAGE
C
      DO 54 J=1,8
      S1(25,J) = 0.0
      S1(26,J) = 0.0
      DO 53 I=1,12
      IF(J.LT.6) GO TO 52
      IF(I.LT.5.OR.I.GT.10) GO TO 53
   52 S1(25,J) = S1(25,J) + S1(I*2-1,J)
      S1(26,J) = S1(26,J) + S1(I*2,J)
   53 CONTINUE
      S1(26,J) = S1(26,J) / 12.0
      IF(J.GT.5) S1(26,J) = S1(26,J) * 2.0
   54 CONTINUE
      DO 56 J=1,5
      S2(25,J) = 0
      S2(26,J) = 0
      DO 55 I=1,12
      S2(25,J) = S2(25,J) + S2(I*2-1,J)
   55 S2(26,J) = S2(26,J) + S2(I*2,J)
   56 S2(26,J) = S2(26,J) / 12.0
      DO 58 J=1,24
      S3(13,J) = 0.0
      DO 57 I=1,12
   57 S3(13,J) = S3(13,J) + S3(I,J)
   58 S3(13,J) = S3(13,J) / 12.0
      WRITE(6,160) IYEAR, IYEAR
      WRITE(6,161)
C
C     WRITE SUMMARY PAGE
C
      DO 61 I=1,12
      K = I * 2 - 1
      L = K + 1
      IF(I.LT.5.OR.I.GT.10) GO TO 60
      WRITE(6,162) (MONTH(I,J),J=1,3), (S1(K,J),J=1,5),S1(K,8), S2(K,5),
     A             (S1(L,J),J=1,7), (S2(L,J),J=1,3), S1(L,8), S2(L,4),
     B             S2(L,5)
      GOTO 61
   60 WRITE(6,163) (MONTH(I,J),J=1,3), (S1(K,J),J=1,5),S2(K,5),
     A             (S1(L,J),J=1,5), (S2(L,J),J=1,5)
   61 CONTINUE
      WRITE(6,164) (S1(25,J),J=1,5), S1(25,8), S2(25,5),
     A             (S1(26,J),J=1,7), (S2(26,J),J=1,3), S1(26,8),
     B             (S2(26,J),J=4,5)
C
      WRITE(6,165) IYEAR, IYEAR
      WRITE(6,166)
      WRITE(6,167) ((MONTH(I,J),J=1,3), (S3(I,K),K=1,12), I=1,13)
      WRITE(6,168)
      WRITE(6,167) ((MONTH(I,J),J=1,3), (S3(I,K),K=13,24), I=1,13)
      WRITE(6,169)
      GOTO 1
C
C
  999 STOP
  120 FORMAT('0',T23,'PRECIPITATION (MM)',T65,'SOIL MOISTURE',T90,
     A        'RELATIVE',/,T7,'DAY',T90,'HUMIDITY    HRS OF      POT',5X,
     B        'CLOUD',/,T7,'OF       TOTAL   RAIN',3(4X,'SNOW'),T60,
     C        'IRRIGATED',T76,'NON-IRRIG',T102,'98-100      EVAP',4X,
     D        'COVER   WIND',/,' DAY  YEAR',3(4X,'PREC'),'     FALL',4X,
     E        'COVER',5X,'PERCENT DEW IRR*  PERCENT DEW    MAX  MIN',4X,
     F        'REL-HUM    (MM)     (0-10)  (KM)',//)
   121 FORMAT('-TOTALS    ',5F8.1,F11.1,2I4,F10.1,I4,T109,F8.1,7X,I8)
   122 FORMAT('0MEANS     ',5F8.1,F11.1,T73,F8.1,T88,2I5,I8,F11.1,I7,I8,/,
      A         '0EXTREMES ',/,
      B         '         HIGH',5F8.1,F11.1,T73,F8.1,T88,2I5,I8,F11.1,I7,I8,/,
      C         '         LOW ',5F8.1,F11.1,T73,F8.1,T88,2I5,I8,F11.1,I7,I8,/,
      D         '-* DATE OF IRRIGATION (MAY THROUGH OCTOBER)')
   123 FORMAT('-TOTALS    ',5F8.1,T124,I8)
   124 FORMAT('0MEANS     ',5F8.1,T88,2I5,I8,11X,I7,I8,/,'0EXTREMES',/,
      A         '         HIGH',5F8.1,T88,2I5,I8,11X,I7,I8,/,
      B         '         LOW ',5F8.1,T88,2I5,I8,11X,I7,I8,/,'-* DATE OF ',
      C         'IRRIGATION (MAY THROUGH OCTOBER)')
   130 FORMAT(31X,'WEATHER SHELTER TEMPERATURES',          32X,'5 CM BENE
      AATH SOIL SURFACE',//,9X,'DAY',13X,'THERMOMETER',16X,'HYGROTHERMOGR
      BAPH',16X,'IRRIGATED',18X,'NON-IRRIGATED',/,9X,'OF',/,5X,
      C 'DAY YEAR',4(8X,'MAX.     MIN.     MEAN '),/)
   131 FORMAT         (5X,A2,2X,A3,4(5X,3F8.1))
   132 FORMAT('-     MEANS  ',4(5X,3F8.1),/,'0    EXTREMES',/,
      A         8X,'HIGH',4(5X,2F8.1,4X,A4),/,8X,'LOW ',4(5X,2F8.1,4X,A4),
      B         /,'-    ALL TEMPERATURES IN DEGREES CELSIUS')
   140 FORMAT(16X,'WEATHER SHELTER',15X,'SOIL SURFACE UNDER GRASS COVER',
      A  27X,'BARE SOIL SURFACE',//,5X,'DAY',10X,'THERMOMETER',4X,
      B  2(11X,'IRRIGATED',14X,'NON-IRRIGATED',3X),/,5X,'OF',/,
      C ' DAY YEAR',6X,'MAX.   MIN.   MEAN',4(7X,'MAX.   MIN.   MEAN'),/)
   141 FORMAT         (1X,A2,2X,A3,5(4X,3F7.1))
   142 FORMAT('-MEANS  ',5(4X,3F7.1),/,'0EXTREMES',/,'    HIGH',
      A         5(4X,2F7.1,3X,A4),/,'    LOW ',5(4X,2F7.1,3X,A4),/,
      B         '-ALL TEMPERATURES IN DEGREES CELSIUS')
   160 FORMAT('1  ',I4,' SUMMARY - PRECIPITATION',95X,'PART 1',///,51X,
      A  I4,' SUMMARY OF METEOROLOGIC DATA',/,55X,'BYU PARASITOLOGY STATI
      BON',/,61X,'PROVO, UTAH',//)
   161 FORMAT(32X,'PRECIPITATION (MM)',T66,'SOIL MOISTURE',T84,
      A         'RELATIVE',/,T68,'(PERCENT)',T84,'HUMIDITY',T97,
      B         'HRS OF   POT    CLOUD',/,24X,'TOTAL   RAIN',
      C         3('     SNOW'),T97,'98-100   EVAP   COVER   WIND',/,3X,
      D         'MONTH',16X,3('PREC     '),'FALL    COVER    IRRG  ',
      E         'NON-IRRG   MAX    MIN    REL HUM  (MM)   (0-10)  (KM)')
   162 FORMAT('0  ',3A4,'TOTAL',5F8.1,5(6X,'--'),F8.1,6X,'--',I8,/,
      A         15X,'MEAN ',7F8.1,3I8,F8.1,2I8)
   163 FORMAT('0  ',3A4,'TOTAL',5F8.1,5(6X,'--'),6X,'ND',6X,'--',I8,/,
      A         15X,'MEAN ',5F8.1,2(6X,'ND'),3I8,6X,'ND',2I8)
   164 FORMAT('-  YEARLY TOTAL        ',5F8.1,5(6X,'--'), F8.1,'*',5X,'--',
      A         I8,/,'0  GRAND MEAN         ',5F8.1,1X,2(F7.1,'*'),I7,2I8,
      3         F8.1,'*',I7,I8,/,'-  ND = NOT DETERMINED',/,'   * CALCULATE
      CD 1 MAY THROUGH 31 OCTOBER ONLY')
   165 FORMAT('1  ',I4,' SUMMARY - TEMPERATURES',95X,'PART 2',///,51X,
      A I4,' SUMMARY OF METEOROLOGIC DATA',/,55X,'BYU PARASITOLOGY STATIO
      BN',/,61X,'PROVO, UTAH',//)
   166 FORMAT(34X,'WEATHER SHELTER TEMPERATURES',          32X,'5 CM BENE
      AATH SOIL SURFACE',//,28X,'THERMOMETER',16X,'HYGROTHERMOGRAPH',16X,
      B'IRRIGATED',18X,'NON-IRRIGATED',/,'0  MONTH',8X,4(8X,'MAX.    MIN.
      C     MEAN '),/)
   167 FORMAT         (12('   ',3A4,4(5X,3F8.1)/),'0  ',3A4,4(5X,3F8.1),//)
   168 FORMAT('-',32X,'SOIL SURFACE UNDER GRASS COVER',34X,'BARE SOIL SUR
      AFACE',//,11X,2(18X,'IRRIGATED',18X,'NON-IRRIGATED'),/,'0  MONTH',
      B   7X,4(9X,'MAX.    MIN.    MEAN'),/)
   169 FORMAT('-  ALL TEMPERATURES IN DEGREES CELSIUS',/,'1')
   200 FORMAT(20I4)
   201 FORMAT(A2,A3,F3.2,4F3.1,2A1,2F3.1,A1,2I3,I2,F3.1,I2,I3,
      A         /,5X,16F3.0)
         END


         SUBROUTINE HEAD (IYEAR,M,IPG,MONTH)
C
C        WRITE A HEADING AND PAGE NUMBER FOR EACH MONTH
C
         INTEGER  NDAYS, DAY, DYR, DEW1, IRRG, DEW2, HHUM, LHUM, THRS,
        A         CLCV, WIND, LINE(10), LIN1(2), LIN2(2), MONTH(13,3)
         REAL     TPRE, RAIN, PRSN, SNOW, SNCV, MOSI, MOSN, PEVP
         COMMON   NDAYS, DAY(31), DYR(31), TPRE(35), RAIN(35), PRSN(35),
        A         SNOW(35), SNCV(35), MOSI(35), DEW1(32), IRRG(32),
        B         MOSN(35), DEW2(32), HHUM(35), LHUM(35), THRS(35),
        C         PEVP(35), CLCV(35), WIND(35)
      WRITE(6,100) (MONTH(M,I),I=1,3), IYEAR, IPG, (MONTH(M,I),I=1,3),
     A             IYEAR
      RETURN
C
      ENTRY PRINTL (I,II)
C
C     PRINTL FORMATS DAILY DATA FOR PRINTING
C     INCLUDES SCALING AND SUPPRESSING ZERO RESULTS
C
      CALL ALPHA (TPRE(I), LINE(1), 25.4)
      CALL ALPHA (RAIN(I), LINE(3), 25.4)
      CALL ALPHA (PRSN(I), LINE(5), 25.4)
      CALL ALPHA (SNOW(I), LINE(7), 25.4)
      CALL ALPHA (SNCV(I), LINE(9), 25.4)
      CALL ALPHA (MOSI(I), LIN1(1), 1.0)
      CALL ALPHA (MOSN(I), LIN2(1), 1.0)
      IF(II.LT.5.OR.II.GT.10) GOTO 2
      WRITE(6,101) DAY(I), DYR(I), LINE, LIN1, DEW1(I), IRRG(I),
     A             LIN2, DEW2(I), HHUM(I), LHUM(I), THRS(I), PEVP(I),
     B             CLCV(I), WIND(I)
      RETURN
    2 WRITE(6,102) DAY(I), DYR(I), LINE, HHUM(I), LHUM(I), THRS(I),
     A             CLCV(I), WIND(I)
      RETURN
C
  100 FORMAT('1   ',2A4,A2,I4,108X,'PAGE ',I1,///,49X,'MONTHLY SUMMARY O
     AF METEOROLOGIC DATA',/,55X,'BYU PARASITOLOGY STATION',/,61X,
     B'PROVO, UTAH',//,60X,2A4,A2,I4,/)
  101 FORMAT(1X,A2,3X,A4,5(2X,A4,A2),6X,A4,A2,2(3X,A1),4X,A4,A2,3X,A1,
     A       3X,2I5,I8,F11.1,I7,I8)
  102 FORMAT(1X,A2,3X,A4,5(2X,A4,A2),T88,2I5,I8,T117,I7,I8)
      END


      SUBROUTINE ALPHA (R,C,S)
C
C     CONVERT R SCALED BY S INTO ALPHA CHARACTERS AND RETURN IN C.
C     (RETURNS BLANK CHARACTERS IF ZERO)
C
      INTEGER N1(301) /'   0','   1','   2','   3','   4','   5','   6',
     A   '   7','   8','   9','  10','  11','  12','  13','  14','  15',
     B   '  16','  17','  18','  19','  20','  21','  22','  23','  24',
     C   '  25','  26','  27','  28','  29','  30','  31','  32','  33',
     D   '  34','  35','  36','  37','  38','  39','  40','  41','  42',
     E   '  43','  44','  45','  46','  47','  48','  49','  50','  51',
     F   '  52','  53','  54','  55','  56','  57','  58','  59','  60',
     G   '  61','  62','  63','  64','  65','  66','  67','  68','  69',
     H   '  70','  71','  72','  73','  74','  75','  76','  77','  78',
     I   '  79','  80','  81','  82','  83','  84','  85','  86','  87',
     J   '  88','  89','  90','  91','  92','  93','  94','  95','  96',
     K   '  97','  98','  99',' 100',' 101',' 102',' 103',' 104',' 105',
     L   ' 106',' 107',' 108',' 109',' 110',' 111',' 112',' 113',' 114',
     M   ' 115',' 116',' 117',' 118',' 119',' 120',' 121',' 122',' 123',
     N   ' 124',' 125',' 126',' 127',' 128',' 129',' 130',' 131',' 132',
     O   ' 133',' 134',' 135',' 136',' 137',' 138',' 139',' 140',' 141',
     P   ' 142',' 143',' 144',' 145',' 146',' 147',' 148',' 149',' 150'/
      INTEGER N3(275) /' 151',' 152',' 153',' 154',' 155',' 156',' 157',
     A   ' 158',' 159',' 160',' 161',' 162',' 163',' 164',' 165',' 166',
     B   ' 167',' 168',' 169',' 170',' 171',' 172',' 173',' 174',' 175',
     C   ' 176',' 177',' 178',' 179',' 180',' 181',' 182',' 183',' 184',
     D   ' 185',' 186',' 187',' 188',' 189',' 190',' 191',' 192',' 193',
     E   ' 194',' 195',' 196',' 197',' 198',' 199',' 200',' 201',' 202',
     F   ' 203',' 204',' 205',' 206',' 207',' 208',' 209',' 210',' 211',
     G   ' 212',' 213',' 214',' 215',' 216',' 217',' 218',' 219',' 220',
     H   ' 221',' 222',' 223',' 224',' 225',' 226',' 227',' 228',' 229',
     I   ' 230',' 231',' 232',' 233',' 234',' 235',' 236',' 237',' 238',
     J   ' 239',' 240',' 241',' 242',' 243',' 244',' 245',' 246',' 247',
     K   ' 248',' 249',' 250',' 251',' 252',' 253',' 254',' 255',' 256',
     L   ' 257',' 258',' 259',' 260',' 261',' 262',' 263',' 264',' 265',
     M   ' 266',' 267',' 268',' 269',' 270',' 271',' 272',' 273',' 274'/
      EQUIVALENCE (N1(152),N3(1))
      INTEGER N2(11)  /'.0','.1','.2','.3','.4','.5','.6','.7','.8',
     A                '.9'/, BLANK/'    '/ , C(2)
      R = R * S
      C(1) = BLANK
      C(2) = BLANK
      R1 = R + 0.05
      I1 = R1
      I2 = (R1 - I1) * 10
      IF(I1.EQ.0.AND.I2.EQ.0) RETURN
      C(1) = N1(I1+1)
      C(2) = N2(I2+1)
      RETURN
      END


      SUBROUTINE CALC (X,N)
C
C     CALC PROCESSES REAL DATA IN X AND RETURNS SUMS IN ROW 32,
C     MEANS IN ROW 33, MINIMUMS IN ROW 34, AND MAXIMUMS IN ROW 35.
C
      REAL X(34,N), S(35)
      REAL BLANK/'    '/
      LOGICAL ZERO
      COMMON NDAYS
      DO 10 J=1,N
      X(32,J) = 0.0
      X(33,J) = -100.0
      X(34,J) = 1000.0
      DO 10 I=1,NDAYS
      IF(MOD(J,3).NE.0) GO TO 9
      X(I,J) = (X(I,J-2) + X(I,J-1)) / 2.0
      X(32,J) = X(32,J) + X(I,J)
      GO TO 10
    9 X(32,J) = X(32,J) + X(I,J)
      IF(X(33,J).LT.X(I,J)) X(33,J) = X(I,J)
      IF(X(34,J).GT.X(I,J)) X(34,J) = X(I,J)
   10 CONTINUE
      DO 11 J=1,N
      X(32,J) = X(32,J) / NDAYS
      IF(MOD(J,3).NE.0) GO TO 11
      X(33,J) = BLANK
      X(34,J) = BLANK
   11 CONTINUE
      RETURN
C
      ENTRY SUMR (S)
C
C     PROCESS REAL DATA IN ARRAY S AND RETURN SUM IN S(32), MEAN IN
C     S(33), MINIMUM IN S(34), AND MAXIMUM IN S(35).
C
      ZERO = .FALSE.
    1 S(32) = 0.0
      S(33) = 0.0
      S(34) = -1000.0
      S(35) = 1000.0
      N = 0
      DO 2 I=1,NDAYS
      IF(ZERO.AND.S(I).LT.0.001) GOTO 2
      N = N + 1
      S(32) = S(32) + S(I)
      IF(S(34).LT.S(I)) S(34) = S(I)
      IF(S(35).GT.S(I)) S(35) = S(I)
    2 CONTINUE
      IF(N.EQ.0) RETURN
      S(33) = S(32) / N
      RETURN
C
      ENTRY SUMZ (S)
      ZERO = .TRUE.
      GOTO 1
      END


      SUBROUTINE SUMI (IY)
C
C     PROCESS INTEGER DATA IN ARRAY IY AND RETURN SUM IN IY(32),
C     MEAN IN IY(33), MINIMUM IN IY(34), AND MAXIMUM IN IY(35).
C
      INTEGER IY(35), PLUS/'+'/
      COMMON NDAYS
      IY(32) = 0
      IY(34) = 0
      IY(35) = 1000
      DO 13 I=1,NDAYS
      IY(32) = IY(32) + IY(I)
      IF(IY(34).LT.IY(I)) IY(34) = IY(I)
      IF(IY(35).GT.IY(I)) IY(35) = IY(I)
   13 CONTINUE
      IY(33) = IY(32) / NDAYS + 0.5
      RETURN
C
C
      ENTRY SUMC (IY)
C
C     PROCESS CHARACTER DATA IN ARRAY IY AND RETURN THE NUMBER OF '+'
C     IN IY(32).
C
      IY(32) = 0
      DO 14 I=1,NDAYS
      IF(IY(I).EQ.PLUS) IY(32) = IY(32) + 1
   14 CONTINUE
      RETURN
      END
```

```
C     ******************************************************************
C     *                                                                *
C     *       WEATHER DATA ANALYSIS, PART II                           *
C     *                                                                *
C     *       PROGRAMMED BY PAUL ROSS ROPER                            Q
C     *                     EYRING RESEARCH INSTITUTE, 1974            *
C     *                                                                *
C     ******************************************************************
C
C
C
C     DECK FORMAT       CONTROL CARD
C                       DATA HEADER    (ON TAPE IF DESIRED)
C                       DATA           (ON TAPE IF DESIRED)
C
C                       COLUMNS   DESCRIPTION
C     1. CONTROL CARD   1-4       YEAR
C                       5-8       DESIRED GRAPH BY NUMBER
C                       9-12 ...  13 GRAPHS POSSIBLE
C
C     2. DATA HEADER    1-4       YEAR OF DATA
C                       5-8       NUMBER OF DAYS IN YEAR
C                       9-12      LAST WIND READING OF PREVIOUS YEAR
C
C     3. DATA           SEE PUBLICATION FOR CARD COLUMNS AND DATA
C                       DESCRIPTION.
C
      COMMON /PLOT0 /  XPLT(366), ITAPE
     A       /PLOT1 /  RAIN(366), XIRR(366), YIRR(366), YNIR(366)
     B       /PLOT2 /  SNOW(366)
     C       /PLOT3 /  YHHD(366), YLHD(366)
     D       /PLOT4 /  HUMD(366)
     E       /PLOT5 /  EVAP(366)
     F       /PLOT6 /  WIND(366)
     G       /PLOT7 /  YMAX(366), YMIN(366)
     H       /PLOT8 /  YH5C(366), YL5C(366), ZH5C(366), ZL5C(366)
     I       /PLOT9 /  YHA1(366), YLA1(366)
     J       /PLOT10/  YHSS(366), YLSS(366), ZHSS(366), ZLSS(366)
     K       /PLOT11/  YHA2(366), YLA2(366)
     L       /PLOT12/  YHBG(366), YLBG(366), ZHBG(366), ZLBG(366)
     M       /PLOT13/  YHA3(366), YLA3(366)
      COMMON /LABELS/  AX1(37), AY1(37), AX2(73), AY2(73),
     A                 BX(4),   BY(4),   XL(4),   YL(4),
     B                 RC1(7),  LC1(7),  RC2(13), LC2(13),
     C                 RC3(11), LC3(11), RC4(13), LC4(13),
     D                 RC5(11), LC5(18), RC6(8),  LC6(16),
     E                 RC7(12), LC7(24)
C
C     CREATE A DEGREE SYMBOL
```

```
      DIMENSION        DEG(3), O(3), NGRAPH(14)
      DATA    DEG      /Z05061727, Z36352414, Z05061727/, J /Z91/
      DATA    O        /Z01061737, Z46413010, Z01061737/, K /Z06/
      CALL SYMBL5 (J,9,DEG)
      CALL SYMBL5 (K,9,O)
      REWIND ITAPE
C
C     READ CONTROL CARD
C
  100 READ(5,200,END=999) NYEAR, NGRAPH
  200 FORMAT(15I4)
      NUM = 0
C
C     READ ONE YEAR'S DATA
C
      CALL READC (NYEAR,NDAYS)
C
C     CONTROL LOOP
C
  300 NUM = NUM + 1
      M = NGRAPH(NUM)
      GO TO (1,2,3,4,5,6,7,8,9,10,11,12,13), M
      GO TO 100
  999 CALL PLOT   (12.0,0.0,-3)
      STOP
C
C
C*****************PLOT   1**************************************************
C                      PRECIPITATION AND SOIL MOISTURE
C
C
    1 CALL  AXES   (3.0,RC1,4,0.5,7,1,LC1,4,0.5,7,1)
      CALL  SCALE  (RAIN,NDAYS,3.00,  3.0,  0.0, 2)
      CALL  SYMBL4 (-0.24,1.2,0.07,'MILLIMETERS',90.0,11)
      CALL  SYMBL4 (0.2,2.8,0.1,'PRECIPITATION',0.0,13)
      CALL  SYMBL4 (1.39,2.8,0.07,'AND',0.0,3)
      CALL  SYMBL4 (1.64,2.8,0.1,'SOIL MOISTURE',0.0,13)
      CALL  DATE   (NYEAR,0.2,2.65)
      CALL  BAR    (XPLT,RAIN,NDAYS)
      CALL  SYMBL4 (8.21,1.3,0.07,'INCHES',90.0,6)
      CALL  MOIST
      GO TO 300
C
C
C*****************PLOT   2**************************************************
C                      SNOW COVER
C
C
    2 CALL  AXES   (3.0,RC2,4,0.25,13,1,LC2,4,0.25,13,1)
      CALL  SCALE  (SNOW,NDAYS,3.00, 12.0,  0.0, 3)
      CALL  SYMBL4 (-0.27,1.2,0.07,'MILLIMETERS',90.0,11)
      CALL  SYMBL4 (0.2,2.8,0.1,'SNOW COVER',0.0,10)
      CALL  DATE   (NYEAR,0.2,2.65)
      CALL  BAR    (XPLT,SNOW,NDAYS)
      CALL  SYMBL4 (8.23,1.3,0.07,'INCHES',90.0,6)
      GO TO 300
C
C
C*****************PLOT   3**************************************************
C                      RELATIVE HUMIDITY IN WEATHER SHELTER
C
C
    3 CALL  AXES   (3.0,RC3,4,0.25,11,1,LC3,4,0.25,11,1)
      CALL  SCALE  (YHHL,NDAYS,2.49,100.0,  0.0, 4)
      CALL  SCALE  (YLHD,NDAYS,2.49,100.0,  0.0, 5)
      CALL  SYMBL4 (-0.25,1.1,0.07,'PERCENT',90.0,7)
      CALL  SYMBL4 (0.2,2.8,0.1,'RELATIVE HUMIDITY IN WEATHER SHELTER',
     A              0.0,36)
      CALL  DATE   (NYEAR,0.2,2.65)
      CALL  LEGEND (1,7.0,2.8)
      CALL  LINES  (XPLT,YHHD,NDAYS,0.01,2)
      CALL  DASH   (XPLT,YLHD,NDAYS,0.03)
      CALL  SYMBL4 (8.25,1.1,0.07,'PERCENT',90.0,7)
      GO TO 300
```

```
C*****************PLOT   4*********************************************
C                    DAILY DURATION OF RELATIVE HUMIDITY
C
C
    4 CALL AXES   (3.0,RC4,4,0.21,13,1,LC4,4,0.21,13,1)
      CALL SCALE  (HUMD,NDAYS,2.49, 24.0,  0.0, 6)
      CALL SYMBL4 (-0.22,1.5,0.07,'HOURS',90.0,5)
      CALL SYMBL4 (0.2,2.8,0.1,'DAILY DURATION OF RELATIVE HUMIDITY AT 9
     A8-100(',      0.0,46)
      CALL DATE   (NYEAR,0.2,2.65)
      CALL BAR    (XPLT,HUMD,NDAYS)
      CALL SYMBL4 (8.23,1.5,0.07,'HOURS',90.0,5)
      GO TO 300
C
C
C*****************PLOT   5*********************************************
C                    POTENTIAL EVAPORATION
    5 CALL AXES   (3.0,RC5,4,0.28,11,1,LC5,5,0.35,18,2)
      CALL SCALE  (EVAP,NDAYS,3.00, 20.0,  0.0, 7)
      CALL SYMBL4 (-0.23,1.2,0.07,'MILLIMETERS',90.0,11)
      CALL SYMBL4 (0.2,2.8,0.1,'POTENTIAL EVAPORATION',0.0,21)
      CALL DATE   (NYEAR,0.2,2.65)
      CALL SYMBL4 (2.0,0.5,0.07,'STARTED',0.0,7)
      J = NDAYS - 244
      CALL LINES  (XPLT(J),EVAP(J),184,0.01,2)
      CALL SYMBL4 (7.0,0.5,0.07,'STOPPED',0.0,7)
      CALL SYMBL4 (8.30,1.3,0.07,'INCHES',90.0,6)
      GO TO 300
C
C
C*****************PLOT   6*********************************************
C                    TOTAL WIND 1 METER ABOVE GROUND
C
C
    6 CALL AXES   (3.0,RC6,4,0.42,8,1,LC6,5,0.42,16,2)
      CALL SCALE  (WIND,NDAYS,2.94,175.0,  0.0, 8)
      CALL SYMBL4 (-0.29,1.2,0.07,'KILOMETERS',90.0,10)
      CALL SYMBL4 (0.2,2.8,0.1,'TOTAL WIND 1 METER ABOVE GROUND',0.0,31)
      CALL DATE   (NYEAR,0.2,2.65)
      CALL LINES  (XPLT,WIND,NDAYS,0.01,2)
      CALL SYMBL4 (8.3,1.4,0.07,'MILES',90.0,5)
      GO TO 300
C
C
C*****************PLOT   7*********************************************
C                    TEMPERATURE IN WEATHER SHELTER
C
C
    7 CALL AXES   (4.0,RC7(1),4,0.5,9,1,LC7(1),5,0.5,18,2)
      CALL SCALE  (YMAX,NDAYS,4.00,122.0,-22.0, 9)
      CALL SCALE  (YMIN,NDAYS,4.00,122.0,-22.0,10)
      CALL SYMBL4 (-0.25,1.2,0.07,'TEMPERATURE (JC)',90.0,16)
      CALL SYMBL4 (0.2,3.7,0.1,'TEMPERATURE IN WEATHER SHELTER',0.0,30)
      CALL DATE   (NYEAR,0.2,3.55)
      CALL LEGEND (1,7.0,3.7)
      CALL ZERO   (1.5)
      CALL SYMBL4 (8.32,1.2,0.07,'TEMPERATURE (JF)',90.0,16)
      CALL LINES  (XPLT,YMAX,NDAYS,0.01,2)
      CALL DASH   (XPLT,YMIN,NDAYS,0.02)
      GO TO 300
C
C
C*****************PLOT   8*********************************************
C                    COMPARISON OF MAX AND MIN TEMP 5 CM UNDER 10 CM GRASS
C
C
    8 CALL AXES   (3.0,RC7(3),4,0.6,6,1,LC7(5),5,0.6,12,2)
      CALL SCALE  (YH5C,NDAYS,3.00, 40.0,-10.0,11)
      CALL SCALE  (YL5C,NDAYS,3.00, 40.0,-10.0,12)
      CALL SCALE  (ZH5C,NDAYS,3.00, 40.0,-10.0,13)
      CALL SCALE  (ZL5C,NDAYS,3.00, 40.0,-10.0,14)
      CALL SYMBL4 (-0.25,1.0,0.07,'TEMPERATURE (JC)',90.0,16)
      CALL SYMBL4 (0.2,2.8,0.1,'COMPARISON OF MAXIMUM AND MINIMUM TEMPER
     AATURES',      0.0,46)
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```
      CALL SYMBL4 (0.2,2.7,0.07,'5 CM DEEP IN SOIL UNDER 10 CM GRASS COV
     AER',         0.0,41)
      CALL SYMBL4 (0.2,2.6,0.07,'ON IRRIGATED AND NON-IRRIGATED PLOTS',
     A             0.0,36)
      CALL DATE   (NYEAR,0.2,2.45)
      CALL LEGEND (2,6.75,2.8)
      CALL ZERO   (0.6)
      CALL SYMBL4 (8.32,1.0,0.07,'TEMPERATURE (JF)',90.0,16)
      CALL LINES  (XPLT,YH5C,NDAYS,0.01,3)
      CALL LINE   (XPLT,YL5C,NDAYS,1)
      CALL DASH   (XPLT,ZH5C,NDAYS,0.04)
      CALL DASH   (XPLT,ZL5C,NDAYS,0.02)
      GO TO 300
C
C
C*****************PLOT  9*********************************************
C                      COMPARISON OF MEANS 5 CM UNDER 10 CM GRASS
C
    9 CALL AXES   (3.0,RC7(3),4,0.6,6,1,LC7(5),5,0.6,12,2)
      CALL SCALE  (YHA1,NDAYS,3.00, 40.0,-10.0,15)
      CALL SCALE  (YLA1,NDAYS,3.00, 40.0,-10.0,16)
      CALL SYMBL4 (-0.25,1.0,0.07,'TEMPERATURE (JC)',90.0,16)
      CALL SYMBL4 (0.2,2.8,0.1,'COMPARISON OF DAILY MEAN TEMPERATURES',
     A             0.0,37)
      CALL SYMBL4 (0.2,2.7,0.07,'5 CM DEEP IN SOIL UNDER 10 CM GRASS COV
     AER',         0.0,41)
      CALL SYMBL4 (0.2,2.6,0.07,'ON IRRIGATED AND NON-IRRIGATED PLOTS',
     A             0.0,36)
      CALL DATE   (NYEAR,0.2,2.45)
      CALL LEGEND (3,6.5,2.8)
      CALL ZERO   (0.6)
      CALL LINES  (XPLT,YHA1,NDAYS,0.01,2)
      CALL DASH   (XPLT,YLA1,NDAYS,0.02)
      CALL SYMBL4 (8.32,1.0,0.07,'TEMPERATURE (JF)',90.0,16)
      GO TO 300
C
C
C*****************PLOT 10*********************************************
C                      COMPARISON OF MAX AND MIN TEMP AT SOIL SURFACE
C
   10 CALL AXES   (3.5,RC7(3),4,0.5,8,1,LC7(5),5,0.5,16,2)
      CALL SCALE  (YHSS,NDAYS,3.50, 60.0,-10.0,17)
      CALL SCALE  (YLSS,NDAYS,3.50, 60.0,-10.0,18)
      CALL SCALE  (ZHSS,NDAYS,3.50, 60.0,-10.0,19)
      CALL SCALE  (ZLSS,NDAYS,3.50, 60.0,-10.0,20)
      CALL SYMBL4 (-0.25,1.3,0.07,'TEMPERATURE (JC)',90.0,16)
      CALL SYMBL4 (0.2,3.3,0.1,'COMPARISON OF MAXIMUM AND MINIMUM TEMPER
     AATURES',     0.0,46)
      CALL SYMBL4 (0.2,3.2,0.07,'AT SOIL SURFACE UNDER 10 CM GRASS COVER
     A',           0.0,39)
      CALL SYMBL4 (0.2,3.1,0.07,'ON IRRIGATED AND NON-IRRIGATED PLOTS',
     A             0.0,36)
      CALL DATE   (NYEAR,0.2,2.95)
      CALL LEGEND (2,6.75,3.3)
      CALL ZERO   (0.5)
      CALL SYMBL4 (8.32,1.3,0.07,'TEMPERATURE (JF)',90.0,16)
      CALL LINES  (XPLT,YHSS,NDAYS,0.01,3)
      CALL LINE   (XPLT,YLSS,NDAYS,1)
      CALL DASH   (XPLT,ZHSS,NDAYS,0.04)
      CALL DASH   (XPLT,ZLSS,NDAYS,0.02)
      GO TO 300
C
C
C*****************PLOT 11*********************************************
C                      COMPARISON OF MEANS AT SOIL SURFACE
C
C
   11 CALL AXES   (3.0,RC7(3),4,0.5,7,1,LC7(5),5,0.5,14,2)
      CALL SCALE  (YHA2,NDAYS,3.00, 50.0,-10.0,21)
      CALL SCALE  (YLA2,NDAYS,3.00, 50.0,-10.0,22)
      CALL SYMBL4 (-0.25,1.0,0.07,'TEMPERATURE (JC)',90.0,16)
      CALL SYMBL4 (0.2,2.8,0.1,'COMPARISON OF DAILY MEAN TEMPERATURES',
     A             0.0,37)
      CALL SYMBL4 (0.2,2.7,0.07,'AT SOIL SURFACE UNDER 10 CM GRASS',
     A             0.0,33)
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```
      CALL SYMBL4 (0.2,2.6,0.07,'ON IRRIGATED AND NON-IRRIGATED PLOTS',
     A             0.0,36)
      CALL DATE   (NYEAR,0.2,2.45)
      CALL LEGEND (3,6.5,2.8)
      CALL ZERO   (0.5)
      CALL SYMBL4 (8.32,1.0,0.07,'TEMPERATURE (JF)',90.0,16)
      CALL LINES  (XPLT,YHA2,NDAYS,0.01,2)
      CALL DASH   (XPLT,YLA2,NDAYS,0.02)
      GO TO 300
C
C
C****************PLOT 12********************************************
C                     COMPARISON OF MAX AND MIN ON BARE GROUND
C
C
   12 CALL AXES   (5.0,PC7(2),4,0.5,11,1,LC7(3),5,0.5,22,2)
      CALL SCALE  (YHBG,NDAYS,5.00, 80.0,-20.0,23)
      CALL SCALE  (YLBG,NDAYS,5.00, 80.0,-20.0,24)
      CALL SCALE  (ZHBG,NDAYS,5.00, 80.0,-20.0,25)
      CALL SCALE  (ZLBG,NDAYS,5.00, 80.0,-20.0,26)
      CALL SYMBL4 (-0.25,2.0,0.07,'TEMPERATURE (JC)',90.0,16)
      CALL SYMBL4 (0.2,4.8,0.1,'COMPARISON OF MAXIMUM AND MINIMUM TEMPER
     AATURES',      0.0,46)
      CALL SYMBL4 (0.2,4.66,0.08,'AT SOIL SURFACE ON BARE GROUND ON',
     A             0.0,33)
      CALL SYMBL4 (0.2,4.52,0.08,'IRRIGATED AND NON-IRRIGATED PLOTS',
     A             0.0,33)
      CALL DATE   (NYEAR,0.2,4.37)
      CALL LEGEND (2,6.75,4.8)
      CALL ZERO   (1.0)
      CALL SYMBL4 (8.32,2.0,0.07,'TEMPERATURE (JF)',90.0,16)
      CALL LINES  (XPLT,YHBG,NDAYS,0.01,3)
      CALL LINE   (XPLT,YLBG,NDAYS,1)
      CALL DASH   (XPLT,ZHBG,NDAYS,0.04)
      CALL DASH   (XPLT,ZLBG,NDAYS,0.02)
      GO TO 300
C
C
C****************PLOT 13********************************************
C                     COMPARISON OF MEANS OF BARE GROUND
C
C
   13 CALL AXES   (3.0,PC7(3),4,0.5,7,1,LC7(5),5,0.5,14,2)
      CALL SCALE  (YHA3,NDAYS,3.00, 50.0,-10.0,27)
      CALL SCALE  (YLA3,NDAYS,3.00, 50.0,-10.0,28)
      CALL SYMBL4 (-0.25,1.0,0.07,'TEMPERATURE (JC)',90.0,16)
      CALL SYMBL4 (0.2,2.8,0.1,'COMPARISON OF DAILY MEAN TEMPERATURES',
     A             0.0,37)
      CALL SYMBL4 (0.2,2.7,0.07,'ON BARE GROUND ON IRRIGATED',0.0,27)
      CALL SYMBL4 (0.2,2.6,0.07,'AND NON-IRRIGATED PLOTS',0.0,23)
      CALL DATE   (NYEAR,0.2,2.45)
      CALL LEGEND (3,6.5,2.8)
      CALL ZERO   (0.5)
      CALL SYMBL4 (8.32,1.0,0.07,'TEMPERATURE (JF)',90.0,16)
      CALL LINES  (XPLT,YHA3,NDAYS,0.01,2)
      CALL DASH   (XPLT,YLA3,NDAYS,0.03)
      GO TO 300
      END

      BLOCK DATA
      COMMON /PLOTO /  XPLT(366), ITAPE
     A       /PLOT1 /  RAIN(366), XIRR(366), YIRR(366), YNIR(366)
     B       /PLOT2 /  SNOW(366)
     C       /PLOT3 /  YHHD(366), YLHD(366)
     D       /PLOT4 /  HUMD(366)
     E       /PLOT5 /  EVAP(366)
     F       /PLOT6 /  WIND(366)
     G       /PLOT7 /  YMAX(366), YMIN(366)
     H       /PLOT8 /  YH5C(366), YL5C(366), ZH5C(366), ZL5C(366)
     I       /PLOT9 /  YHA1(366), YLA1(366)
     J       /PLOT10/  YHSS(366), YLSS(366), ZHSS(366), ZLSS(366)
     K       /PLOT11/  YHA2(366), YLA2(366)
     L       /PLOT12/  YHBG(366), YLBG(366), ZHBG(366), ZLBG(366)
     M       /PLOT13/  YHA3(366), YLA3(366)
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0003              COMMON /LABELS/  AX1(37), AY1(37), AX2(73), AY2(73),
                 A                 BX(4),   BY(4),   XL(4),   YL(4),
                 B                 RC1(7),  LC1(7),  RC2(13), LC2(13),
                 C                 RC3(11), LC3(11), RC4(13), LC4(13),
                 D                 RC5(11), LC5(18), RC6(8),  LC6(16),
                 E                 RC7(12), LC7(24)
            C     TAPE UNIT NUMBER
0004              DATA     ITAPE   /5/
0005              DATA     RC1,LC1 /'  0 ', '   -', ' 25-', '   -', ' 50-', '   -',
                 A                  ' 75-', '  0 ', '-   ', '- 1 ', '-   ', '- 2 ',
                 B                  '-   ', '  3 '/
0006              DATA     RC2,LC2 /'  0 ', ' 25-', ' 50-', ' 75-', '100-', '125-',
                 A                  '150-', '175-', '200-', '225-', '250-', '275-',
                 B                  '300-', '  0 ', '- 1 ', '- 2 ', '- 3 ', '- 4 ',
                 C                  '- 5 ', '- 6 ', '- 7 ', '- 8 ', '- 9 ', '- 10',
                 D                  '- 11', '- 12'/
0007              DATA     RC3,LC3 /'  0 ', ' 10-', ' 20-', ' 30-', ' 40-', ' 50-',
                 A                  ' 60-', ' 70-', ' 80-', ' 90-', '100-', '  0 ',
                 B                  '- 10', '- 20', '- 30', '- 40', '- 50', '- 60',
                 C                  '- 70', '- 80', '- 90', '-100'/
0008              DATA     RC4,LC4 /'  0 ', '  2-', '  4-', '  6-', '  8-', ' 10-',
                 A                  ' 12-', ' 14-', ' 16-', ' 18-', ' 20-', ' 22-',
                 B                  ' 24-', '  0 ', '- 2 ', '- 4 ', '- 6 ', '- 8 ',
                 C                  '- 10', '- 12', '- 14', '- 16', '- 18', '- 20',
                 D                  '- 22', '- 24'/
0009              DATA     RC5,LC5 /'  0 ', '  2-', '  4-', '  6-', '  8-', ' 10-',
                 A                  ' 12-', ' 14-', ' 16-', ' 18-', ' 20-', '  0.',
                 B                  '0   ', '- 0.', '1   ', '- 0.', '2   ', '- 0.',
                 C                  '3   ', '- 0.', '4   ', '- 0.', '5   ', '- 0.',
                 D                  '6   ', '- 0.', '7   ', '- 0.', '8   '/
0010              DATA     RC6,LC6 /'  0 ', ' 40-', ' 80-', '120-', '160-', '200-',
                 A                  '240-', '280-', '    ', '0   ', '-  2', '5   ',
                 B                  '-  5', '0   ', '-  7', '5   ', '- 10', '0   ',
                 C                  '- 12', '5   ', '- 15', '0   ', '- 17', '5   '/
0011              DATA     RC7,LC7 /'-30-', '-20-', '-10-', '  0 ', ' 10-', ' 20-',
                 A                  ' 30-', ' 40-', ' 50-', ' 60-', ' 70-', ' 80-',
                 B                  '- -2', '2   ', '-  -', '4   ', '-  1', '4   ',
                 C                  '-  3', '2   ', '-  5', '0   ', '-  6', '8   ',
                 D                  '-  8', '6   ', '- 10', '4   ', '- 12', '2   ',
                 E                  '- 14', '0   ', '- 15', '8   ', '- 17', '6   '/
0012              DATA     BX,BY   /2*0.0, 2*7.94, 4*0.0/
0013              DATA     XL,YL   /3.99, 2*0.0, -0.04, 2*0.0, 2*1.34/
0014              DATA     AX1,AY1 /2*7.94,3*7.27,3*6.61,3*5.94,3*5.29,3*4.61,
                 A                  3*3.94,3*3.29,3*2.61,3*1.96,3*1.28,3*0.67,2*0.0,
                 B                  0.03,2*0.0,0.03,2*0.0,0.03,2*0.0,0.03,2*0.0,
                 C                  0.03,2*0.0,0.03,2*0.0,0.03,2*0.0,0.03,2*0.0,
                 D                  0.03,2*0.0,0.03,2*0.0,0.03,2*0.0,0.03,2*0.0,
                 E                  0.03/
0015              DATA     AX2     /2*7.94,3*7.60,3*7.27,3*6.94,3*6.61,3*6.28,
                 A                  3*5.95,3*5.62,3*5.29,3*4.95,3*4.61,3*4.28,
                 B                  3*3.94,3*3.62,3*3.29,3*2.95,3*2.61,3*2.29,
                 C                  3*1.96,3*1.62,3*1.28,3*0.98,3*0.67,3*0.34,2*0.0/
0016              DATA     AY2     /-0.03,2*0.0,-0.03,2*0.0,-0.03,2*0.0,-0.03,2*0.0,
                 A                  -0.03,2*0.0,-0.03,2*0.0,-0.03,2*0.0,-0.03,2*0.0,
                 B                  -0.03,2*0.0,-0.03,2*0.0,-0.03,2*0.0,-0.03,2*0.0,
                 C                  -0.03,2*0.0,-0.03,2*0.0,-0.03,2*0.0,-0.03,2*0.0,
                 D                  -0.03,2*0.0,-0.03,2*0.0,-0.03,2*0.0,-0.03,2*0.0,
                 E                  -0.03,2*0.0,-0.03,2*0.0,-0.03,2*0.0,-0.03,2*0.0,
                 F                  -0.03/
0017              END


0001              SUBROUTINE AXES   (HT,X,NXC,DX,N1,M1,Y,NYC,DY,N2,M2)
            C
            C     GRAPH A BOX OF HEIGHT HT WITH THE MONTHS PLOTTED ALONG THE BOTTOM.
            C     ALSO LABEL THE BOX WITH ARRAY X ON THE RIGHT AND Y ON THE LEFT.
            C     DX IS THE DISTANCE BETWEEN EACH LABLE.  N1 IS THE NUMBER OF LABELS
            C     AND M1 IS THE STEP BETWEEN LABLES.  THE SAME IS TRUE FOR ARRAY Y
            C     WITH DY, N2, AND M2.
            C
0002              DIMENSION X(N1), Y(N2)
0003              COMMON /LABELS/  AX1(37), AY1(37), AX2(73), AY2(73),
                 A                 BX(4),   BY(4)
0004              DATA     NCOUNT  /1/
```

```
      IF(NCOUNT.NE.1) GO TO 10
      CALL PLOTS (12.0,0.0,-3)
      CALL PLOT  (2.0,1.0,-3)
      GO TO 11
   10 CALL PLOT   (0.0,6.5,-3)
   11 CALL PLTMRK (-2.0,0.0)
      NCOUNT = NCOUNT + 1
      IF(NCOUNT.EQ.5) NCOUNT = 1
      BY(2) = HT
      BY(3) = HT
      CALL SYMBL4 (0.0,0.03,0.07,'  JANUARY   FEBRUARY     MARCH        A
     APRIL       MAY        JUNE        JULY       AUGUST     SEPTEMBER    OC
     BTOBER   NOVEMBER   DECEMBER',0.0,131)
      CALL LINE (AX1,AY1,37,1)
      CALL PLOT (0.0,0.27,-3)
      CALL SYMBL4 (0.0,-0.11,0.07,'1     15     1     15     1     15     1
     A 15     1     15     1     15     1     15     1     15     1     15     1
     B 15     1     15     1     15',0.0,128)
      CALL LINE (AX2,AY2,73,1)
      CALL LINE (BX,BY,4,1)
      DYY = -0.03
      DO 12 I=1,N2,M2
      CALL SYMBL4 (7.9,DYY,0.07,Y(I),0.0,NYC)
      DYY = DYY + DY
   12 CONTINUE
      DXX = -0.03
      DO 13 I=1,N1,M1
      CALL SYMBL4 (-0.22,DXX,0.07,X(I),0.0,NXC)
      DXX = DXX + DX
   13 CONTINUE
      GO TO 14
C
C     DRAW ZERO LINE AT HEIGHT HT.
C
      ENTRY ZERO (HT)
      BY(2) = HT
      BY(3) = HT
      CALL LINE (BX(2),BY(2),2,1)
   14 RETURN
      END
```

```
      SUBROUTINE DASH (X,Y,N,S)
C
C     SUBROUTINE DASH WILL DRAW DASHED LINES
C
C     X = X ARRAY
C     Y = Y ARRAY
C     N = NUMBER OF POINTS
C     S = LENGTH OF DASHES
C
      DIMENSION X(N), Y(N), A(2), B(2)
      SS = S * 2.0
      DO 30 I=2,N
      DX = X(I) - X(I-1)
      DY = Y(I) - Y(I-1)
      H = SQRT(DX*DX + DY*DY)
      DX = S * DX / H
      DY = S * DY / H
      A(1) = X(I-1)
      B(1) = Y(I-1)
   10 CONTINUE
      IF(H.LE.S) GO TO 20
      A(2) = A(1) + DX
      B(2) = B(1) + DY
      CALL LINE (A,B,2,1)
      IF(H.LE.SS) GO TO 30
      A(1) = A(2) + DX
      B(1) = B(2) + DY
      H = H - SS
      GO TO 10
   20 A(2) = X(I)
      B(2) = Y(I)
      CALL LINE (A,B,2,1)
   30 CONTINUE
```

```
      GO TO 99
C
C     SUBROUTINE LINES WILL MAKE THE LINE DARKER AND WIDER BY DRAWING
C            N NUMBER OF LINES
C
C     X = X ARRAY
C     Y = Y ARRAY
C     N = NUMBER OF POINTS
C     D = DISTANCE BETWEEN LINES
C     M = NUMBER OF LINES
C
      ENTRY LINES (X,Y,N,D,M)
      DY = 0.0
      DO 40 I=1,M
      CALL LINE (X,Y,N,1)
      CALL PLOT (0.0,D,-3)
      DY = DY - D
   40 CONTINUE
      CALL PLOT (0.0,DY,-3)
      GO TO 99
      ENTRY BAR (X,Y,N)
      SS = 0.0
      CALL PLOT (X(1),SS,3)
      DO 50 I=2,N
      CALL PLOT (X(I-1),Y(I),1)
      CALL PLOT (X(I),Y(I),1)
   50 CONTINUE
      CALL PLOT (X(N),SS,1)
   99 RETURN
      END
```

```
      SUBROUTINE DATE (NYR,X,Y)
C
C     GRAPH DATE SPECIFIED BY NYR AT POINT (X,Y)
C
      CALL SYMBL4 (X,Y,0.07,'PROVO, UTAH,',0.0,12)
      N = NYR-1969
      GOTO (1,2,3,4,5), N
    1 CALL SYMBL4 (X+0.78,Y,0.07,'1970',0.0,4)
      RETURN
    2 CALL SYMBL4 (X+0.78,Y,0.07,'1971',0.0,4)
      RETURN
    3 CALL SYMBL4 (X+0.78,Y,0.07,'1972',0.0,4)
      RETURN
    4 CALL SYMBL4 (X+0.78,Y,0.07,'1973',0.0,4)
      RETURN
    5 CALL SYMBL4 (X+0.78,Y,0.07,'1974',0.0,4)
      RETURN
C
C
      ENTRY LEGEND (N,X,Y)
C
C     GRAPHS ONE OF FOUR LEGENDS SPECIFIED BY N AT POINT (X,Y)
C
      GOTO (10,11,12,13),N
   10 CALL SYMBL4 (X,Y,0.07,'MAXIMUM',0.0,7)
      CALL SYMBL4 (X,Y-0.1,0.07,'MINIMUM',0.0,7)
      RETURN
   11 CALL SYMBL4 (X,Y,0.07,'MAX NON-IRR',0.0,11)
      CALL SYMBL4 (X,Y-0.1,0.07,'MIN NON-IRR',0.0,11)
      CALL SYMBL4 (X,Y-0.22,0.07,'MAX IRRIGATED',0.0,13)
      CALL SYMBL4 (X,Y-0.32,0.07,'MIN IRRIGATED',0.0,13)
      RETURN
   12 CALL SYMBL4 (X,Y,0.07,'MEAN NON-IRRIGATED',0.0,18)
      CALL SYMBL4 (X,Y-0.1,0.07,'MEAN IRRIGATED',0.0,14)
   13 RETURN
      END
```

```
      SUBROUTINE SCALE (X,N,S,YMAX,YMIN,ID)
C
C     SCALE DATE IN ARRAY X DIMENSIONED BY N AND RETURN SCALED DATA IN
C     Y.  S IS THE MAXIMUM HEIGHT OF SCALED DATA, YMAX HAS MAXIMUM
C     ALLOWED DATA AND YMIN THE MINIMUM.  SHOULD DATA EXCEED THESE
C     BOUNDS, THE ID NUMBER WILL BE PRINTED ALONG WITH THE DATA.
```

```
      DIMENSION X(N)
      SS = S / (YMAX-YMIN)
      DO 10 I=1,N
      IF(X(I).LT.YMIN) WRITE(6,101) ID, X(I), YMIN
      IF(X(I).GT.YMAX) WRITE(6,100) ID, X(I), YMAX
      X(I) = SS * (X(I) - YMIN)
   10 CONTINUE
      RETURN
  100 FORMAT(' CALL ',I2,5X,F10.2,' EXCEEDED ',F9.1)
  101 FORMAT(' CALL ',I2,5X,F10.2,' WAS BELOW ',F8.1)
      END

      SUBROUTINE READC (IYEAR,NDAYS)
C
C     READ ONE YEAR'S DATA SPECIFIED BY IYEAR.  THE FIRST CARD IS A DATA
C     HEADER CONTAINING THE YEAR, NUMBER OF DAYS IN YEAR AND LAST
C     RECORDED WIND VALUE OF PREVIOUS YEAR.  RETURN NUMBER OF DAYS IN
C     NDAYS.
C
      COMMON /PLOT0 /  XPLT(366), ITAPE
     A       /PLOT1 /  TPRE(366), XIRR(366), YIRR(366), YNIR(366)
     B       /PLOT2 /  SNCV(366)
     C       /PLOT3 /  HHUM(366), LHUM(366)
     D       /PLOT4 /  THRS(366)
     E       /PLOT5 /  PEVP(366)
     F       /PLOT6 /  WIND(366)
     G       /PLOT7 /  YMAX(366), YMIN(366)
     H       /PLOT8 /  YH5C(366), YL5C(366), ZH5C(366), ZL5C(366)
     I       /PLOT9 /  YHA1(366), YLA1(366)
     J       /PLOT10/  YHSS(366), YLSS(366), ZHSS(366), ZLSS(366)
     K       /PLOT11/  YHA2(366), YLA2(366)
     L       /PLOT12/  YHBG(366), YLBG(366), ZHBG(366), ZLBG(366)
     M       /PLOT13/  YHA3(366), YLA3(366)
      COMMON /LABELS/  DUMY(228), XL(4),    YL(4)
      REAL     CH(11)  /'  0 ', '    -', ' 10-', '    -', ' 20-', '    -',
     A                   ' 30-', '    -', ' 40-', '    -', ' 50 '/
      REAL HHUM, LHUM, NIWW, NIDW, IRWW, IRDW ,OLDW
      AVE(X,Y) = (X+Y)/2.0
C
    1 READ(ITAPE,200,END=999) IYR,NDAYS,OLDW
  200 FORMAT(2I4,F4.0)
      IF(IYEAR.EQ.IYR) GO TO 3
      DO 2 I=1,NDAYS
    2 READ(ITAPE,200,END=999)
      GO TO 1
C
C
    3 DO 4 I=1,NDAYS
      READ(ITAPE,201,END=999) RAIN, SNOW, SNCV(I), IRWW, IRDW, NIWW,
     A                   NIDW, HHUM(I), LHUM(I), THRS(I), PEVP(I),
     B                   CLCV, WIND(I), YMAX(I), YMIN(I),
     C                   YH5C(I), YL5C(I), YHSS(I), YLSS(I), YHBG(I),
     D                   YLBG(I), ZH5C(I), ZL5C(I), ZHSS(I), ZLSS(I),
     E                   ZHBG(I), ZLBG(I)
  201 FORMAT(5X,F3.2,4F3.1,2X,2F3.1,1X,2F3.0,F2.0,F3.1,F2.0,F3.0,/,
     A       5X,2F3.0,6X,12F3.0)
      XPLT(I) = I
      TPRE(I) = RAIN + SNOW*0.1
      YIRR(I) = -1.0
      YNIR(I) = -1.0
      IF(NIWW.NE.0.0) YNIR(I) = (NIWW-NIDW)*100.0/NIDW
      IF(IRWW.NE.0.0) YIRR(I) = (IRWW-IRDW)*100.0/IRDW
      IF(OLDW.GT.WIND(I)) OLDW = OLDW - 1000.0
      HOLD = WIND(I)
      WIND(I) = (WIND(I)-OLDW) * 1.6093+0.05
      OLDW = HOLD
      YHA1(I) = AVE(YH5C(I),YL5C(I))
      YLA1(I) = AVE(ZH5C(I),ZL5C(I))
      YHA2(I) = AVE(YHSS(I),YLSS(I))
      YLA2(I) = AVE(ZHSS(I),ZLSS(I))
      YHA3(I) = AVE(YHBG(I),YLBG(I))
      YLA3(I) = AVE(ZHBG(I),ZLBG(I))
    4 CONTINUE
      YDAYS = NDAYS
      CALL SCALE (XPLT,NDAYS,7.94,YDAYS,  1.0, 1)
      RETURN
  999 WRITE(6,500)
  500 FORMAT('-********ERROR IN INPUT DATA FROM TAPE *****',//)
      STOP
C
C
      ENTRY MOIST
      CALL PLOT   (0.0,1.2,-3)
      N = 0
      DO 20 I=121,306
      IF(YIRR(I).LT.0.0) GO TO 20
      N = N + 1
      YIRR(N) = YIRR(I)
      XIRR(N) = XPLT(I)
   20 CONTINUE
      CALL SCALE (YIRR,N,1.28,50.0,0.0,29)
      CALL LINE (XIRR,YIRR,N,1)
      N = 0
      DO 30 I=121,306
      IF(YNIR(I).LT.0.0) GO TO 30
      N = N + 1
      XIRR(N) = XPLT(I)
      YNIR(N) = YNIR(I)
   30 CONTINUE
      CALL SCALE (YNIR,N,1.28,50.0,0.0,30)
      CALL DASH (XIRR,YNIR,N,0.04)
      CALL PLOT   (2.61,0.0,-3)
      CALL LINE   (XL,YL,4,1)
      DY = -0.03
      DO 10 I=1,11
      CALL SYMBL4 (-0.22,DY,0.07,CR(I),0.0,4)
      DY = DY + 0.13
   10 CONTINUE
      CALL SYMBL4 (-0.22,0.45,0.07,'PERCENT',90.0,7)
      CALL SYMBL4 (3.2,1.53,0.07,'SOIL MOISTURE (IRRIGATED)',0.0,25)
      CALL SYMBL4 (3.2,1.63,0.07,'SOIL MOISTURE (NON-IRRIGATED)',0.0,29)
      CALL PLOT (-2.61,-1.2,-3)
      RETURN
      END
```

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CLARENCE COTTAM, 1899-1974

A Distinguished Alumnus of Brigham Young University

Vasco M. Tanner[1]

Dr. Clarence Cottam was one of the nation's most outstanding and productive biologists and conservationists. While this is an achievement in itself, he further distinguished himself in the field of administration during his service as assistant director of the U.S. Fish and Wildlife Service between 1945 and 1954, and as director, for almost twenty years, of the Rob and Bessie Welder Wildlife Refuge at Sinton, Texas.

Clarence Cottam was born in Utah's Dixieland at Saint George on January 1, 1899. His father, Thomas P. Cottam, and his mother, Emmaline Jarvis Cottam, were prominent St. George citizens, his father having served as mayor of St. George and counselor with the LDS stake president, Edward H. Snow. He was also a successful farmer and mason. Clarence spent his boyhood days working on the farm and enjoying the plants and animals of the Virgin River and Santa Clara Creek. The St. George area is the sole region of Utah in which the plant and animal species of the Lower Sonoran Zone are found. Clarence became acquainted early with the vermilion flycatcher, gambel quail, roadrunner, phainopepla, and western mockingbird and as a high school student evidenced an interest in and general acquaintance with the birds of his homeland. The following is extracted from one of his papers written in 1970:

> My work in the field of conservation, teaching, and management of resources certainly had its start in the biological training I gleaned under the able leadership of Dr. Tanner at Dixie and BYU.
>
> In my first course in high school biology, Dr. Tanner asked me what species of hummingbirds I had seen. To me they were all hummers, so I answered, "Little hummers; and bigger ones and some had white throats and some with iridescent black and brilliant red throats." He answered kindly but challengingly asked, "What species are here?" and he added "It will be a lot of fun to find out." Then he inquired, "what kind of flowers do they go to?" I could only reply that they came to flowers of different colors and I had seen them in flowers of different shades of red, blue and white. He challenged me further by asking "what do these tiny birds feed on?" I could only suggest "something inside of the flowers." He then assigned me the task of finding out what I could about hummingbirds. There were few books on birds at that time in St. George and still fewer of those dealing with these diminutive but attractive creatures, so he reminded me that the best place to learn of them was out of nature, he appropriately added that nature's books were always open at the appropriate time.
>
> I doubt that my esteemed friend and teacher has the faintest recollection of this little incident, and I am still more sure that any knowledge I imparted on this assignment was elementary indeed. Still, this challenging excursion into nature left an indelible impression on my mind. It has over the years made me ask many questions about nature's ways and her varied progeny. How do they survive and compete? What good or harm do they do? What relationship do they have to their environment and to other species? Why were they where I found them? How could they be increased, decreased or controlled? What were the basic factors of their population dynamics?
>
> In looking back on these rich early experiences I feel that the most valuable training I received was on our summer field trip when we were collecting insects, birds, rodents, and plants for the University. On these trips the graduate students were collecting and studying specific groups of organisms or problems for their respective theses. I was studying and collecting birds.[2]

After completing his school work at Dixie College, Clarence was called to spend two years in the central states as a missionary for the LDS Church. In 1922 he accepted the principalship of the schools at Alamo, Nevada, and in 1925 he matriculated at Brigham Young University and was appointed an instructor in bi-

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[2] Great Basin Nat. 30:201. 1970.

Fig. 1. Clarence Cottam, 1899-1974.

ology. For the next four years he was active in research and field work. He graduated with a B.S. degree in zoology and entomology in 1926 and a year later was awarded a Master of Science degree. His thesis dealt with the birds of Utah.

In 1929 Clarence received an appointment as junior biologist in the U.S. Bureau of Biological Survey in Washington, D.C. During his first few years with the Bureau he devoted himself to an investigation of food habits research but also found time to continue graduate studies at George Washington University, from which he received a Ph.D. degree in 1936. This early study resulted in his most prized contribution, "Food habits of North American diving ducks" (1936). At this time Clarence also became closely associated with leaders and authorities on wildlife management and conservation such as Ira N. Gabrielson, Aldo Leopold, and J. N. (Ding) Darling. Embracing their point of view, he became one of this country's most dynamic and sought after champions of wildlife conservation.

Clarence was an ambitious, friendly individual. He made friends with the officials of organizations and societies throughout the United States, Canada, and some foreign countries that were concerned with the flora and fauna of the nation. He was a fluent speaker, well informed on the management of wildlife. Few, if any, conservationists of the Clarence Cottam era were his peers in promulgating conservation measures in behalf of the wildlife of our country. He vigorously opposed the indiscriminate use of certain poisons for the control of insects, birds, fish, and mammals and spoke out against destroying food and nesting habitats of native fish and birds through the drainage of wet lands and dredging and contamination of the nation's waterways.

During Dr. Cottam's 25-year affiliation with the U.S. Biological Survey, later the U.S. Fish and Wildlife Service, many organizations sought after his services as a consultant or officer. He was president of the Wildlife Society (1949-1950), Texas Ornithological Society (1957-1959), and National Parks Association (1962-1963); trustee of the J. N. (Ding) Darling Foundation and the Rachel Carson Trust. He was an active member of the following organizations: American Ornithological Union, Cooper Ornithological Society, Wilson Ornithological Society, Forestry Association, Outdoor Writers Association, Wildlife Management Institute, Izaak Walton League, Cosmos Club, Soil Conservation Society, Friends of the Land, Wildlife Society, Utah Academy of Sciences, Arts, and Letters, American Association for the Advancement of Science, Ecological Society of America, Limnological Society, American Society of Mammalogists, American Society of Range Management, National Wildlife Federation, National Audubon Society, Sigma Xi, Sierra Club, American Institute of Biological Sciences, and the Southwestern Association of Naturalists.

In recognition of his leadership and counsel as an untiring government official and stimulating member of many societies, he was the recipient of the following awards: the Leopold Medal from the Wildlife Society (1955); Utah State University Distinguished Service Award (1957); National Audubon Society Distinguished Service Medal (1961); Conservation Service Citation of the National

Wildlife Federation (1964); Distinguished Service Award, BYU (1964); Conservation Service Award of the Department of the Interior (1965); Distinguished Service Award of the Texas Chapter of the Wildlife Society (1971); "Eminent Distinction" status in the National Register of Prominent Americans and International Notables (1971); James A. Talmage Scientific Achievement Award, BYU (1971); Distinguished Service Award of the Texas Ornithological Society (1972).

In 1954 Clarence resigned his government post to accept the deanship of the College of Biological and Agricultural Science at Brigham Young University. As dean, he had begun instituting a number of significant changes in the college when he received an offer to become the director of the Welder Wildlife Foundation at Sinton, Texas—a new and promising project. Because this program provided many possibilities for research and the means of demonstrating what must be done to develop conservation measures for the perpetuity of many of the country's plant and animal species, Dr. Cottam accepted the directorship, assuming his duties as director of the Rob and Bessie Welder Wildlife Foundation in 1955.

For almost 20 years Clarence directed the development of the Welder Wildlife Refuge on the Aransas River in San Patricio County, near Sinton, Texas. The refuge, located in a transition zone between coastal prairie and the Rio Grande plain, is a strip of rich alluvial land, seven miles long and about two miles wide. For many years it was part of a cattle ranch, and today as a part of the biota of the refuge there are more than 500 head of beef cattle.

The refuge is favorably located to serve as a conservation research area. Dr. Cottam observed that "this is one of the richest areas for flora and fauna in America."[3] In this wilderness he has identified more than 1,300 species of plants, including 200 species of grass and more than 400 species of birds. Through the efforts of Dr. Cottam and his staff the refuge has been developed into one of the most renowned wildlife research and educational laboratories in the United States. Nearly 150 students from many universities have obtained graduate degrees under leadership at the foundation.

Dr. Cottam was a bibliophile; he built up a complete set of ornithological journals and textbooks on American birds for the use of students at the refuge. He was also concerned with the migration, breeding, and feeding of game birds and campaigned for the protection of rare and vanishing species, such as hawks, owls, eagles, whooping cranes, and brown pelicans. He constantly emphasized the necessity of having a broad, well-grounded program, based upon verifiable facts, when dealing with conservation problems.

Clarence also found time to coauthor, with Dr. Angus M. Woodbury and John Sudgen, a manuscript dealing with the birds of Utah. The untimely, accidental death of Dr. Woodbury, the senior author, delayed the publication of this important treatise. Through the efforts of Dr. Cottam this manuscript was turned over to Dr. C. Lynn Hayward of the Department of Zoology at BYU to review, edit, and publish.

Clarence had the help and companionship of a gracious, artistic helpmate and wife, Margery Brown Cottam, whom he married on May 20, 1920, while they were both teaching at Alamo, Nevada. They were the parents of four girls: Glenna, Mrs. Ivan L. Sanderson of San Francisco, California; Margery, Mrs. Grant Osborne, Amherst, Massachusetts; Josephine, Mrs. Douglas S. Day, Salt Lake City, Utah; and Caroline, Mrs. Dwayne Stevenson, McClaine, Virginia. They had 23 grandchildren and 4 great grandchildren. Margery was an active member of the LDS Church, serving as stake YWMIA president and stake Relief Society president. She died February 28, 1975, and was buried beside Clarence at Orem, Utah.

Always religious and devoted to the LDS Church, Dr. Cottam was a pillar of strength in the LDS Corpus Christi (Texas) Stake. He served as first counselor in the San Antonio Stake, after which he served for nine years as president of the Corpus Christi Stake. At the time of his death, March 30, 1974, he was patriarch of the Corpus Christi Stake.

He was the essence of tolerance in his dealings with his fellowmen. As an educator, administrator, researcher, and intermediary between scientific groups and the the sports public, Dr. Cottam was most successful.

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[3] Deseret News, 16 June 1973, Church Section, p. 7.

Dr. Clarence Cottam's name is indelibly inscribed on the roster of distinguished alumni of Brigham Young University. For the past 50 years I have enjoyed watching him become one of the most honored biologists of the nation.

The long list of his publications which follows reveals his wide experience and insight in providing solutions to man's mistakes in dealing with his animate environment.

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EVOLUTIONARY DIVERGENCE IN CLOSELY RELATED POPULATIONS OF MIMULUS GUTTATUS (SCROPHULARIACEAE)[1]

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ABSTRACT.— The evolutionary divergence of five closely related populations of the yellow monkey flower, *Mimulus guttatus*, was compared with the length of time the populations could have occupied the site and with the ability of the populations to intercross. Populations from the younger sites were found to be morphologically intermediate to populations from the older sites. Ability to intercross was not correlated with morphological divergence at this stage of evolution.

Glaciation patterns of the Wasatch Mountains of Utah provide an estimate of the geological age of existing plant populations. If evolutionary relationships between isolated populations can be determined, an estimate of rates of evolution for these populations may be obtained. The purpose of this investigation is to determine the amount of divergence between populations from previously glaciated and unglaciated sites and to relate this divergence to the age and possible origin of the populations. Divergence is estimated by calculating a Prim network (Prim, 1957), based on morphological characteristics of the populations, and by analyzing the ability of the populations to intercross. The Prim network was calculated for 24 morphological traits and for 6 selected traits to determine whether larger numbers of characters make a significant difference in the network.

METHODS AND MATERIALS

Five populations of *Mimulus guttatus* Fischer ex D.C., the yellow monkey flower, from two adjacent canyon drainages were selected for investigation (Table 1). *M. guttatus* grows in small isolated populations near streams or springs and is thus ideal for studies of evolutionary divergence. Plants were grown from seeds in the greenhouse. Quantitative data were gathered for 24 morphological traits on an average of 16 plants per population. We were unable to select a larger number of traits because of the close morphological relationships of the populataions. Traits selected include height, dry weight, degree of pigmentation, timing and extent of flowering and seed set, etc. (Crook, 1964). Plants from each population were intercrossed in all combinations but one, i.e., diallel design.

The estimated age of the populations was determined from the period of time each site was available, geologically, for occupation by the populations. The Thousand Springs and Storm Mountain sites have never been glaciated and apparently have been available for occupation for 50,000 years or more, while the remaining three sites were glaciated and have been available only since the retreat of the Wisconsin period glaciers (Table 2). Populations may not be as old as the site and may have migrated up and down the mountainsides with changing environmental conditions at the end of the glacial epoch.

TABLE 1. Populations of *Mimulus guttatus*

Culture number	Location
6648	Big Water Gulch, Millcreek Canyon. Along stream south of parking lot at end of road. Altitude 7,680 feet.
5840	Thousand Springs, Millcreek Canyon. Hillside adjacent to road. Site is marked with a road sign. Altitude 7,200 feet.
6649	Brighton Loop. Big Cottonwood Canyon on Clayton Peak drainage. East edge of Brighton Loop at top of canyon. Altitude 8,760 feet.
5839	Spruces, Big Cottonwood Canyon. Stream and marsh areas of Spruces Campground. Altitude 7,360 feet.
6127	Storm Mountain, Big Cottonwood Canyon. Stream in small canyon south of Storm Mountain Campground. Altitude 6,240 feet.

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[1] This investigation was supported in part by a Public Health Service Fellowship (No. D-F1-GM-19, 725-07) from the Division of General Medical Sciences, Public Health Service.

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TABLE 2. Maximum estimates of time available for occupation of sites by *Mimulus guttatus* populations.

Site	Most recent glaciation
Brighton	9,000 years before present*
Spruces	11,000 years before present*
Storm Mountain	Not glaciated
Big Water Gulch	11,000 years before present*
Thousand Springs	Not glaciated

* Deglaciation occurred later than these dates.

The 24 morphological traits were analyzed by the principal components method of factor analysis as outlined by Harman (1964) to obtain factors composed of mutually correlated groups of traits. Six major factors were obtained with eigenvalues greater than one (Crook, 1964).

The morphological similarities of the populations were determined by calculations of a shortest distance network developed by Prim (1957) and adapted to evolutionary studies by Edwards and Cavalli-Sforza (1964). In this method the sum of the normalized character differences between the populations is the estimate of the difference. Populations with large numbers of differing traits are widely separated on the network and vice versa. The assumption implicit in the use of the Prim network for evolutionary studies is that the sum of the character differences is proportional to the evolutionary differences between the populations. It should be noted that Edwards and Cavalli-Sforza made assumptions of independence and selective neutrality not made here. The assumption of neutrality is not necessary, as we are interested in divergence, whether random or the result of selective pressures. The 24 morphological traits are clearly not independent, as they may be combined into 6 groups of mutually correlated traits by factor analysis. Some of the 24 variables are represented in more than one factor (Crook, 1964). The 6 traits are as independent as can be obtained in that they represent high factor loading on one factor and very low loadings on the other factors. Prim networks were calculated for all 24 characters and for the 6 characters obtained from factor analysis.

RESULTS AND DISCUSSION

The 6 major factors derived from the factor analysis of 24 characters can be identified as follows. Factor 1 is a composite factor representing general bushiness of the plant, with high factor loadings on the number of leaves and branches and on measurements related to the age of the plant. Factor 2 represents dry-weight measurements, with emphasis on roots and runners. Factor 3 represents almost entirely pigment measurements, with negative loadings on age. Factor 4 is a general measure of height. Factor 5 is a general measure of flower size. Factor 6 has the highest loadings on duration of flowering and seed set. The characteristic with the highest factor loading in each factor was selected for analysis by the Prim network (Table 3).

The Prim networks based on 24 morphological characters and on the 6 selected morphological characters are given in Figures 1 and 2. Both networks are identical in pattern, but the distances between populations vary somewhat.

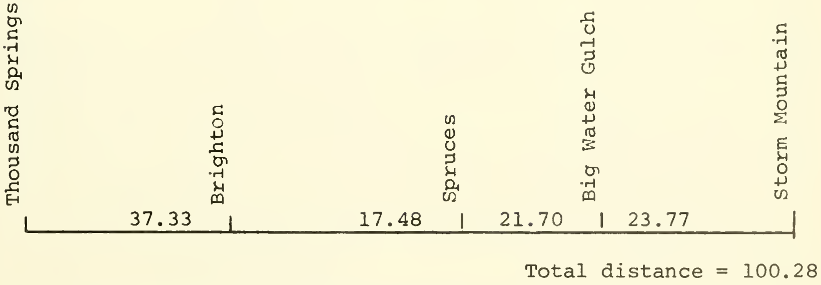

Fig. 1. Prim network for 24 morphological traits.

TABLE 3. Morphological traits selected by factor analysis.

1. Total number of branches at end of seed production
2. Total dry weight recorded at end of seed production
3. Number of internodes on main stem that show anthocyanin pigment
4. Length in mm of longest internode
5. Length of last flower produced by the plant
6. Time in days of seed production

All populations tested intercrossed. In only two cases was the seed production reduced (Figure 3). Thousand Springs ♀ X Spruces ♂ produced an average of 89 seeds per capsule. Spruces ♀ X Brighton ♂ produced an average of 90.61 seeds per capsule. The average parental seed production for all populations in the study was 173.67. Big Water Gulch and Thousand Springs were not intercrossed.

The correlation of Prim network distances between populations and the number of seeds produced was not significant when Prim network distance was calculated from all 24 traits (r= −.026) and barely significant when Prim network distance was calculated from 6 traits (r= −.443, p=.05).

CONCLUSION

The similarity of the two Prim networks indicates that fewer characteristics may be used without distorting the observed pattern of relationships between the populations; however, the distances between populations do change somewhat. In this study the characteristics for the second network were selected by factor analysis; however, the factors represented broad generalized categories, and an investigator with an extensive knowledge of his/her organism might intuitively select similarly representative factors. Factor analysis might also be used in a preliminary study by investigators who lack resources for collecting large amounts of data.

In both Prim networks the oldest populations, i.e., populations occupying sites that have been available for the longest period of time, appear at either end of the network, while populations from the newer sites occupy intermediate positions. This finding is in agreement with the pattern of evolution expected if the younger populations received portions of their gene pool from the older established populations. Mimulus is an edible plant, and Lindsay (1960) has shown that seeds can pass undigested through the digestive tract of birds. It is thus possible that birds and mammals could carry the seeds from site to site. Seeds deposited in recently deglaciated sites would find little competition from other plants and would be likely to survive. Seeds carried to well-established older sites from the younger sites would have to compete with well-adapted genotypes. Thus the younger populations are likely to be a mixture of genotypes from the older populations, while the older populations would tend to maintain their well-adapted genotypes. If this pattern of evolution is correct, we would expect that the younger populations would be a mixture of genotypes from the older, well-established populations and would be intermediate to the older populations on the Prim network. The network suggests that older popula-

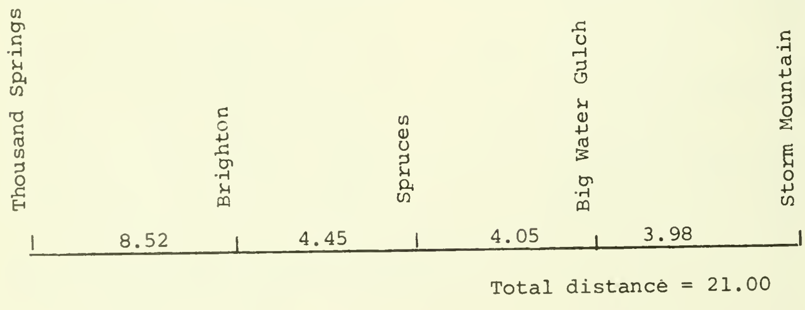

Fig. 2. Prim network for six morphological traits.

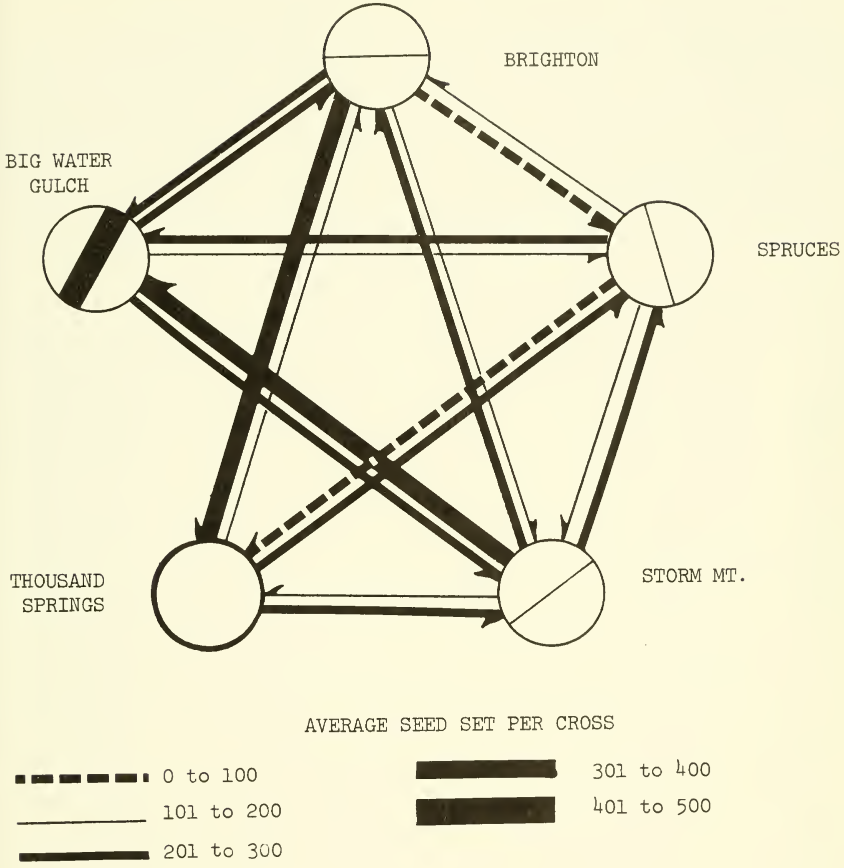

Fig. 3. Seeds produced by crosses between populations of *Mimulus guttatus*. The direction of the arrow is from male pollen donor to female. Crosses within populations are indicated by a bar within the circle. Self-pollinations are indicated by the thickness of the circle circumference.

tions are more closely related to the younger populations in adjacent canyons than to younger populations in the same canyon. This may reflect the results of selection on a mixture of genotypes rather than patterns of population establishment.

The failure of crossing data to correlate with the Prim network results is not surprising. None of the populations have shown significant morphological differences, and barriers to gene exchange have not evolved. At such a point a random accumulation of gene differences might or might not cause a reduction in ability to intercross, depending upon which genes are involved.

SUMMARY

Prim networks based on 24 and 6 morphological traits were identical with respect to order of the populations. However, the distances between the populations did vary from population to population. The two oldest populations appeared at either end of the network, while the more recently established populations ap-

peared in the middle. Probably the older, well-adapted populations donated a portion of their gene pools to the younger populations.

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GREAT BASIN NATURALIST

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Subscriptions. The annual subscription is $9 (outside the United States $10). The price for single numbers is $3 each. All back numbers are in print and are available for sale. All matters pertaining to the purchase of subscriptions and back numbers should be directed to Brigham Young University Press, Marketing Department, 204 UPB, Provo, Utah 84602.

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The Great Basin Naturalist

Published at Provo, Utah, by
Brigham Young University

Volume 35 September 30, 1975 No. 3

UROSAURUS AND ITS PHYLOGENETIC RELATIONSHIP TO *UTA* AS DETERMINED BY OSTEOLOGY AND MYOLOGY (REPTILIA: IGUANIDAE)

Charles Fanghella[1], David F. Avery[2], and Wilmer W. Tanner[3]

Abstract.— The status of the genus *Urosaurus* Hallowell and its relationship to the genus *Uta* Baird and Girard as presented in previous studies are reviewed. Additional data from the head and throat osteology and myology are included in the analysis. Each bone and muscle is measured, ratios determined, and the position noted. Five distinct anatomical differences are noted between *Uta* and *Urosaurus*, and it is concluded that both of these genera are sufficiently different to warrant generic status. *Uta* is considered to be phylogenetically more primitive.

The climbing utas (*Urosaurus*) and the the ground utas (*Uta*) are two genera which have had an uncertain systematic relationship. Studies by Mittleman (1942), Savage (1958), Etheridge (1962), and Larsen and Tanner (1975) have used various sets of morphological data to explain their affinities, but myological characteristics have been mostly neglected. Other studies involving taxonomy by Balanger and Tinkle (1973) and Tanner and Jorgensen (1963), ecology and external anatomy by Smith (1946), Tinkle (1967), Turner et al. (1970), and Tanner (1972), of *Uta* and *Urosaurus* and other related genera have been done. However, the validity of the genus *Urosaurus* and its position in the phylogeny of the Iguanidae has not been completely established. The present study is designed to investigate the anterior osteological and myological anatomy of these genera in order to determine their relationship to each other and to show their phylogenetic position in the family Iguanidae.

The literature dealing with the anatomy of iguanid lizards has been reviewed by Avery and Tanner (1971); therefore, we will confine our study primarily to problems relating to phylogeny. Data from previous studies, as indicated above, will be added to our myological findings.

Baird and Girard (1852) erected the genus *Uta* for the species *stansburiana*, which was characterized by gular folds, auricular openings, and a fine, homogeneous dorsal scalation. Later that year they described another form, *Uta ornata*, which differed from *stansburiana* in having the dorsal scalation composed of fine, strongly keeled, prominently imbricated scales which were divided into two parallel series on either side of the median dorsal line by a series of somewhat smaller, vertebral scales. However, Hallowell (1854) encountered a different lizard similar to *Uta ornata* Baird and Girard. It had enlarged dorsals extending the length of the dorsum in a broad and uninterrupted band and lacked the smaller, dividing series of scales. For this species Hallowell established the genus *Urosaurus*. Dumeril (1856) described the genus *Phymatolepsis* for a species similar to *Uta ornata* in that it has similar dorsals on either side of the smaller vertebral scales. These actions were challenged by Baird (1858) who described *Uta symmetrica*, a close relative of *Uta ornata*; and the next year he (Baird, 1859) placed Hallowell's *Urosaurus* in synonomy with *Uta* because of similar dorsal scalation and prominently characterized gular folds. *Urosaurus* was used as a subgenus by Van Denburgh (1922). *Phymatolepsis* was placed in synonomy under *Uta* by Cope (1864). Although Fischer (1882) and Boulenger (1883) used the name, it was again placed in synonomy by Boulenger (1885).

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Cope (1863) described the distinctive *Uta thalassina* from a general habitat sufficiently different from other known forms that Boulenger (1885) considered it generically distinct and proposed the name *Petrosaurus*. Boulenger's usage was ignored by Cope (1887), who retained *Uta thalassina*. Except for Van Denburgh (1922), who used *Petrosaurus* subgenerically, the name has been considered a synonym of *Uta*.

Mittleman (1942) reviewed the phylogenetic relationships of North American iguanid genera and considered *Ctenosaura* (Wiegmann, 1828) to have evolved from a primitive iguanid genus and to have given rise to two phyletic lines. The first contains *Crotaphytus* (Holbrook, 1842), and the other sceloporine line contains the following genera: *Uta* (Baird and Girard, 1852), *Urosaurus* (Hallowell, 1854, and *Sator* (Dickerson, 1919). *Uta* and *Urosaurus* are considered to have evolved from an early progenitor related to *Sceloporus*, which soon diversified sufficiently to produce *Uta* and *Urosaurus*. The latter genus is probably the older of the two. *Uta* probably did not disperse until the beginning of the Miocene, for it is restricted to the continental United States and Mexico and many of the adjoining islands. According to Mittleman (1942) *Uta* and *Urosaurus* " . . . may be considered as very nearly biological equivalents, for they are widely distributed, highly prolific, of about the same age, successful, and derived from closely related progenitors."

Sator (Dickerson, 1919), because of its relationship with *Sceloporus*, is also of interest. Although Dickerson (1919) mentioned certain osteological characteristics unique to *Sator*, the constant osteological variations within the genera *Sator*, *Sceloporus*, *Uta*, and *Urosaurus* have not been properly ascertained. Mittleman (1942) designates *Sator* as a direct derivative of the primitive *pyrocephalus* group of *Sceloporus* and considers it to be not closely related to any other lizard.

Stejneger and Barbour (1943) and Smith and Taylor (1950), in their checklist of lizards of the U.S. and Mexico, adopted Mittleman's (1942) arrangement of the "utas," while Smith (1946) presented a somewhat modified phylogeny of North American iguanids that is, nevertheless, in basic agreement with Mittleman's work. Since Mittleman's study, herpetologists have been divided in their acceptance of his work as opposed to that of Oliver (1943), who did not recognize Mittleman's genera because he saw few characters separating them. Oliver retained all the species now assigned to either *Uta* or *Urosaurus* within the genus *Uta*. Schmidt (1953) and Stebbins (1954), among others, adhered to his view. Mittleman's classification was based upon his interpretation of external characteristics rather than upon marked structural differences between the several species groups.

Savage (1958) is in general agreement with Mittleman's two lines of phylogeny: the iguanine line and the sceloporine line. However, genera placed in the sceloporine line by the two authorities do not agree. Savage states that based upon the type of sternal arrangement there are two major subdivisions within the sceloporine group. Within the line having a utiform sterum, two distinct stocks are indicated. One of these is represented by the genus *Phrynosoma*, which lacks xiphisternal ribs. The other group, with the utiform sterum bearing xiphisternal ribs, contains the genera *Callisaurus*, *Holbrookia*, *Uma*, and *Uta*. Within *Uta*, the subgenus *Petrosaurus* is considered by Savage to be the most primitive, although highly adapted for a rock habitat. The genera *Urosaurus*, *Sator*, and *Sceloporus* are closely allied and differ from the other sceloporines in having a urosaurine type of sternum which possesses xiphisternal ribs. Thus in Savage's studies, based upon the type of sternal arrangements, *Uta* and *Urosaurus* are distinctly different genera.

Presch (1969) reports that the osteological characteristics indicate that the horned lizards (*Phrynosoma*) form a highly specialized genus within the *Sceloporus* group of genera (*Sceloporus*, *Sator*, *Uta*, *Urosaurus*, *Uma*, *Callisaurus*, *Holbrookia*, and *Petrosaurus*). *Phrynosoma* is distinguished from all other members of the family in having both a large sternal fontanelle and femoral pores. He lists *Petrosaurus* as primitive because of its moderately sized sternal fontanelle and the presence of four sternal ribs. Of the two groups derived from *Petrosaurus*, the least altered are *Urosaurus*, *Uta*, *Sceloporus*, and *Sator*, which have hooks on the clavicle and a covering over the anterolateral processes of the frontal in some species, while *Holbrookia*, *Uma*, and *Callisaurus* are the most highly evolved. They have lost the lacrimal and postfrontal bones and the first pair of cervical ribs. Also, the interclavicle is shortened, and the anterolateral processes of the frontal are covered. Thus *Uta* and *Urosaurus* are placed in the same group but in distinctly different genera.

Etheridge (1964) claims tthat osteological comparisons do not provide a strong enough argument for or against the recognition of *Uta* and *Urosaurus* as separate genera. However, the few osteological differences between sceloporines that do exist suggest that three subgroups might be recognized: (1) *Holbrookia*, *Callisaurus*, and *Uma* with two cervical ribs (three in all others); (2) *Uta*, *Urosaurus*, *Sator*, and *Sceloporus* with clavicular hooks present (absent in all others); and (3) *Petrosaurus* with four sternal ribs (two or three in others).

Hotton (1955) in his studies of dentition and food habits has implied that although *Uta* and *Urosaurus* are interpreted as direct but independent descendants of sceloporines, the dentition and diet of the utas are similar to *Callisaurus*. Lowe (1955) studied the problem of generic status of *Uta* and *Urosaurus* using ecological relationships. He was able to recognize genera on the basis of ecologic divergence alone, without the support of any other character.

On this ecological concept Lowe and Norris (1955) based their classification of the assemblage of lizards formerly placed in the genus *Uta*. They confirmed Mittleman's arrangement of these species because of supporting ecological differences between and similarities within the groups involved. As a result of their studies, they recognized the following taxonomic arrangement: genus *Petrosaurus* with subgenus *Streptosaurus*; genus *Uta* and genus *Urosaurus*.

Petrosaurus and *Streptosaurus* were placed together because of their cliff-dwelling habits. *Urosaurus* was retained as a distinct genus because the species within the group are plant dwellers and climbers. *Uta* was distinguished from the other two genera by its ground-dwelling life-style.

Mittleman's classification of these iguanids has not been generally accepted by Savage and others because he failed to present convincing evidence that the several groups were morphologically different from one another. The most striking morphological feature listed by Mittleman as separating *Uta* from *Urosaurus* was the homogeneous scutellation of the former and the differentiation of the paravertebral scales in the latter.

We extend our gratitude to those who have helped us in the preparation of this paper. We are grateful to Dr. Ernest Williams, at the Department of Herpetology, Museum of Comparative Zoology at Harvard, for providing us with various prepared skeletons of *Uta* and *Urosaurus*. We also thank Mr. Chester J. Bosworth and Dr. Dwight G. Smith, who have been so kind as to read and criticize this study, distribute necessary literature, and make suggestions. We are grateful to Kenneth R. Larsen and Wilmer W. Tanner for making available a copy of the manuscript of Larsen and Tanner (1975). Lastly we thank Southern Connecticut State College for financial aid and the loan of materials and space for part of this study, and Brigham Young University for editorial and publication courtesies.

MATERIALS AND METHODS

Skeletons used in the study were borrowed from the Museum of Comparative Zoology at Harvard (MCZ), and preserved specimens were borrowed from Southern Connecticut State College (SCSC).

One skeleton of *Urosaurus ornata wrighti* and three of *Uta s. stansburiana* were prepared by carefully stripping away the skin, connective fascia, and large muscle the first day of skeletonizing. After drying, the remaining tissues were removed by stripping and picking until the skeletons were clean.

All measurements were taken in millimeters with an ocular micrometer mounted in a dissecting microscope. All measurements were taken from the extreme points of the width and length of each structure.

Specimens are accessioned in the natural history collection of MCZ and/or

SCSC. The materials utilized for this study are as follows:

Osteology

Uta stansburiana stansburiana Baird and Girard
MCZ 62443, Utah
SCSC 381, East of Elberta, Utah
SCSC 382, East of Elberta, Utah
SCSC 383, East of Elberta, Utah
Urosaurus ornata symmetrica (Baird)
MCZ 26695, Fort Yuma, Arizona
Urosaurus ornata linearis (Baird)
MCZ 04947, Tucson Mt. Park, Arizona
Urosaurus ornata lateralis (Boulenger)
MCZ 14345, Guaymas, Mexico
Urosaurus ornata schotti (Baird)
MCZ 64122, Sonora, Southern Guaymas, Mexico
Urosaurus ornata wrighti Schmidt
SCSC 384, Moab, Utah

Myology

Uta stansburiana stansburiana Baird and Girard
SCSC 381, Utah County, Utah
SCSC 382, Utah County, Utah
SCSC 383, Utah County, Utah
Urosaurus ornata (Baird)
SCSC 921, Moab, Utah
SCSC 922, Moab, Utah
SCSC 923, Moab, Utah

OSTEOLOGY

A study of the osseous elements of *Uta* and *Urosaurus* reveals a basic pattern that was described by Savage (1958), Ethridge (1964), and Avery and Tanner (1971) for these and other iguanids. As a result we confine our descriptions to deviations from that pattern.

Skull and Jaws

An analysis of the skull and jaw was made from data obtained by examining their size and shape. After skulls were measured, a percentage was computed between length and width and compared with similar data for both genera. Measurements and ratios were taken for identical bones in both genera. Those bones having an average mean greater than 40 points are presented in Tables 1 and 2. venience of reference the skull has been subdivided into a posterior occipital unit and an anterior maxillary unit.

The skulls are streptostylic with a freely movable quadrate bone which ar-

TABLE 1.— Minimum, mean, and maximum measurements and ratios for the skull structures of *Uta*.

Name of structure	Length Min. Mean Max.	Width Min. Mean Max.	Width-length ratio Min. Mean Max.
Basisphenoid	1.22 - 1.35 - 1.46	1.71 - 1.83 - 1.95	.715 - .767 - .775
Basioccipital	1.46 - 1.75 - 2.14	2.20 - 2.46 - 2.78	.640 - .701 - .770
Pterygoid	3.95 - 4.58 - 5.12	1.27 - 1.62 - 2.30	.274 - .354 - .445
Ectopterygoid	2.20 - 2.26 - 2.44	1.61 - 1.77 - 1.95	.700 - .704 - .885
Vomer	1.76 - 1.92 - 2.04	.780 - .830 - .880	.400 - .431 - .472
Palatine	1.71 - 1.92 - 2.10	.975 - 1.18 - 1.22	.500 - .579 - .687
Premaxilla	1.42 - 1.86 - 2.44	1.46 - 1.67 - 2.24	.600 - .733 - 1.00
Maxilla	4.78 - 5.08 - 5.60	1.95 - 1.99 - 2.04	.352 - .396 - .416
Nasal	1.80 - 1.97 - 2.04	.486 - .658 - .975	.239 - .332 - .476
Prefrontal	2.39 - 2.62 - 2.88	.490 - 1.41 - 1.90	.202 - .433 - .710
Lacrimal	.487 - .574 - .684	.390 - .573 - .732	.072 - .101 - .150
Frontal	3.90 - 4.07 - 4.35	3.66 - 4.02 - 4.64	.842 - .903 - .940
Postorbital	1.07 - 1.92 - 2.62	1.66 - 1.79 - 1.95	.550 - .711 - .925
Jugal	6.10 - 6.58 - 7.22	.440 - .610 - .732	.070 - .092 - .104
Parietal	3.24 - 3.86 - 4.10	5.15 - 5.66 - 5.90	.630 - .680 - .717
Postfrontal	.487 - .682 - .926	.098 - .195 - .293	.154 - .288 - .400
Squamosal	2.30 - 2.60 - 2.93	.685 - .844 - 1.07	.250 - .325 - .390
Quadrate	.735 - .811 - .975	1.95 - 2.32 - 2.44	.314 - .346 - .410
Supratemp. Fossa	2.78 - 2.91 - 3.04	1.12 - 1.36 - 1.51	.104 - .467 - .505
Orbit	4.35 - 4.41 - 4.50	3.17 - 3.37 - 3.47	.720 - .762 - .820
Nasal Opening	.975 - 1.38 - 1.61	1.02 - 1.15 - 1.42	.635 - .770 - .995
Dentary	6.60 - 7.08 - 7.80	.972 - 1.15 - 1.22	.125 - .163 - .185
Articular	3.16 - 3.46 - 3.86	.586 - .720 - .880	.172 - .207 - .243
Angular Pr.	5.70 - 6.89 - 9.50	4.77 - 6.07 - 7.15	.750 - .824 - .855
Surangular	2.20 - 3.17 - 4.14	.440 - .598 - .780	.151 - .185 - .214
Splenial	2.20 - 2.42 - 2.58	.195 - .242 - .585	.075 - .174 - .226
Angular	5.70 - 6.89 - 9.50	1.43 - 1.88 - 2.30	.214 - .280 - .334
Coronoid	2.20 - 3.23 - 4.40	1.46 - 1.67 - 2.04	.388 - .560 - .926
Pyriform Recess	2.68 - 3.17 - 3.42	2.04 - 2.27 - 2.44	.700 - .722 - .765
Parasphenoid Pr.	.925 - 1.21 - 1.46	.487 - .487 - .487	.331 - .424 - .525
Entire Skull	11.2 - 11.6 - 11.9	6.35 - 7.26 - 8.05	.566 - .623 - .675

TABLE 2.— Minimum, mean, and maximum measurements and ratios for the skull structures of *Urosaurus*.

Name of structure	Length Min. Mean Max.	Width Min. Mean Max.	Width-length ratio Min. Mean Max.
Basisphenoid	1.56 - 1.71 - 1.95	1.90 - 2.01 - 2.14	.800 - .872 - 1.00
Basioccipital	1.22 - 1.57 - 1.80	2.68 - 2.89 - 3.17	.455 - .555 - .675
Pterygoid	4.00 - 4.74 - 5.37	1.17 - 1.32 - 1.46	.280 - .304 - .366
Ectopterygoid	1.41 - 1.84 - 2.24	1.17 - 1.50 - 1.80	.655 - .753 - .880
Vomer	1.22 - 1.76 - 2.44	.733 - .811 - .930	.340 - .488 - .680
Palatine	1.46 - 1.84 - 2.20	.975 - 1.24 - 1.71	.445 - .848 - 1.00
Premaxilla	1.22 - 1.44 - 1.56	1.71 - 2.23 - 2.58	.565 - .656 - .730
Maxilla	5.26 - 5.84 - 6.10	2.20 - 2.21 - 2.34	.360 - .405 - .437
Nasal	2.04 - 2.32 - 2.78	.830 - .946 - 1.07	.360 - .410 - .464
Prefrontal	2.74 - 2.91 - 3.12	1.07 - 1.22 - 1.36	.344 - .419 - .462
Lacrimal	.487 - .615 - .737	.487 - .615 - .732	.073 - .286 - 1.00
Frontal	3.80 - 4.15 - 4.40	4.40 - 4.60 - 4.87	.780 - .902 - .990
Postorbital	2.44 - 2.75 - 3.18	1.71 - 1.86 - 1.95	.538 - .688 - .800
Jugal	5.37 - 6.00 - 6.35	.540 - .635 - .732	.088 - .106 - .127
Parietal	3.90 - 4.08 - 4.30	5.35 - 5.64 - 5.96	.661 - .723 - .765
Postfrontal	.585 - .791 - .975	.024 - .190 - .440	.024 - .255 - .500
Squamosal	2.44 - 2.55 - 2.93	.780 - .940 - 1.07	.327 - .370 - .440
Quadrate	.930 - 1.07 - 1.32	2.20 - 2.34 - 2.64	.405 - .460 - .590
Supratemp. Fossa	2.78 - 3.14 - 3.36	1.32 - 1.54 - 1.76	.430 - .448 - .525
Orbit	3.90 - 4.59 - 4.90	3.42 - 3.68 - 3.90	.720 - .806 - .875
Nasal Opening	1.49 - 1.52 - 1.61	.585 - .975 - 1.22	.388 - .656 - .897
Dentary	6.84 - 7.15 - 7.60	.810 - .889 - .928	.118 - .124 - .131
Articular	3.26 - 3.44 - 3.76	.974 - 1.39 - 1.85	.300 - .399 - .507
Angular Pr.	5.70 - 6.30 - 7.15	5.70 - 6.77 - 8.10	.705 - .875 - 1.00
Surangular	2.68 - 2.86 - 3.26	.684 - .794 - .880	.225 - .271 - .328
Splenial	2.20 - 2.53 - 2.92	.244 - .478 - .585	.084 - .156 - .244
Angular	5.70 - 6.30 - 7.15	1.43 - 1.03 - 1.90	.252 - .284 - .333
Coronoid	2.68 - 2.96 - 3.18	1.27 - 1.73 - 1.95	.400 - .591 - .726
Pyriform Recess	2.44 - 2.76 - 3.18	1.76 - 2.08 - 2.44	.635 - .760 - .910
Parasphenoid Pr.	.925 - 1.25 - 1.42	.440 - .597 - .925	.360 - .474 - .650
Entire Skull	11.2 - 11.6 - 12.4	6.75 - 7.38 - 7.80	.582 - .633 - .670

ticulates dorsally with the paroccipital process and ventrally with the quadrate process of the pterygoid. Thus, they form a compact, light, and strong cage for the brain and sense organs.

The actual shape of the skull is either elongated and flattened dorsoventrally, as in *Uta*, or shortened and laterally compressed, as in *Urosaurus*. Measurements of the length of the skull were from the top of the premaxillary bone to the most posterior extension of the occipital condyle. Measurements of the width were from the widest extension between the suborbital bars in the area of the orbit.

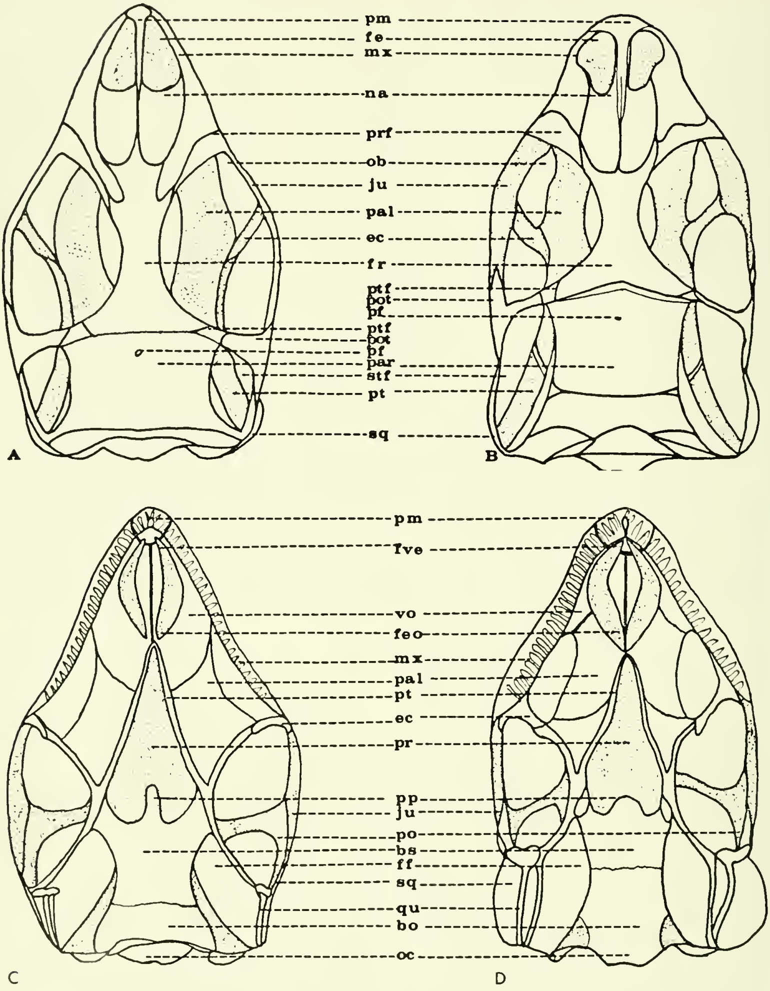
The means in Tables 1 and 2 indicate that *Uta* has a slightly lower skull ratio (.623) than *Urosaurus* (.633). For con-

The occipital portion forms a median wall for the attachment of the neck and articulation for the remainder of the skull. It consists of two parts: (a) braincase (basisphenoid, basioccipital, prootic, exoccipital, supraoccipital) (b) foramen magnum (enclosed by the basioccipital, exoccipitals, and supraoccipital). A tripartate occipital condyle is located on the posterior end of the basioccipital and the lateral exoccipital in all iguanine genera.

Basisphenoid: Length is from the suture between basisphenoid and basioccipital, to the beginning of the parasphenoid process (Fig. 1). Width is the distance between the widest expansion of the basioptygoid processes. The lowest ratio mean is in *Uta* (.767), the highest in *Urosaurus* (.872). A low ratio indicates that the bone is much longer than it is wide, whereas the higher ratios indicate bones with lengths and widths more nearly equal.

Basioccipital: Length is from the suture between the basisphenoid and basioccipital to the posterior tip of the occipital condyle (Fig. 1); and width is between the tips of the lateral extensions of the sphenoccipital tubercles. The ratio in *Uta* is .701 and *Urosaurus* .555.

Pterygoid: Length (Figs. 1, 2, 3) is between the anterior portion of the pterygoid where it sutures with the palatine and the most posterior tip of the quadrate process. Width is between the articulation with the basipterygoid process of the basisphen-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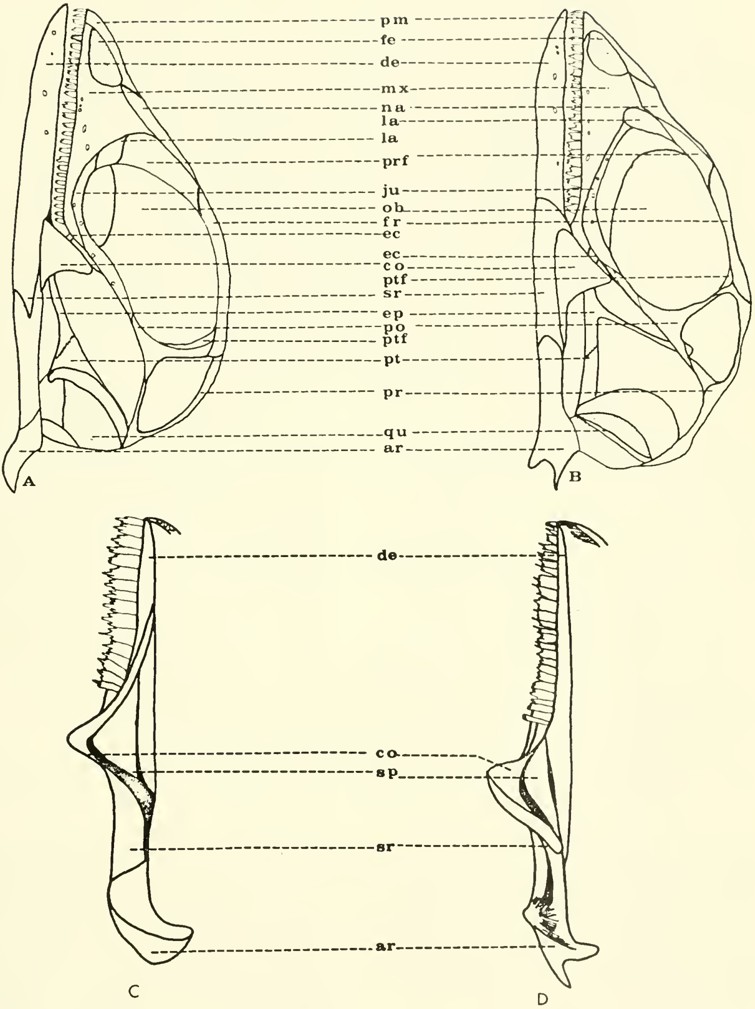
PF—Pineal foramen
PM—Premaxilla
POT—Postorbital
PP—Parasphenoid process
PR—Pyriform recess
PRF—Prefrontal
PT—Pterygoid
PTF—Postfrontal
QU—Quadrate
STF—Supratemporal fossa
SQ—Squamosal
VO—Vomer

Fig. 1. Dorsal and ventral views of skulls. A and C *Uta*, B and D *Urosaurus*.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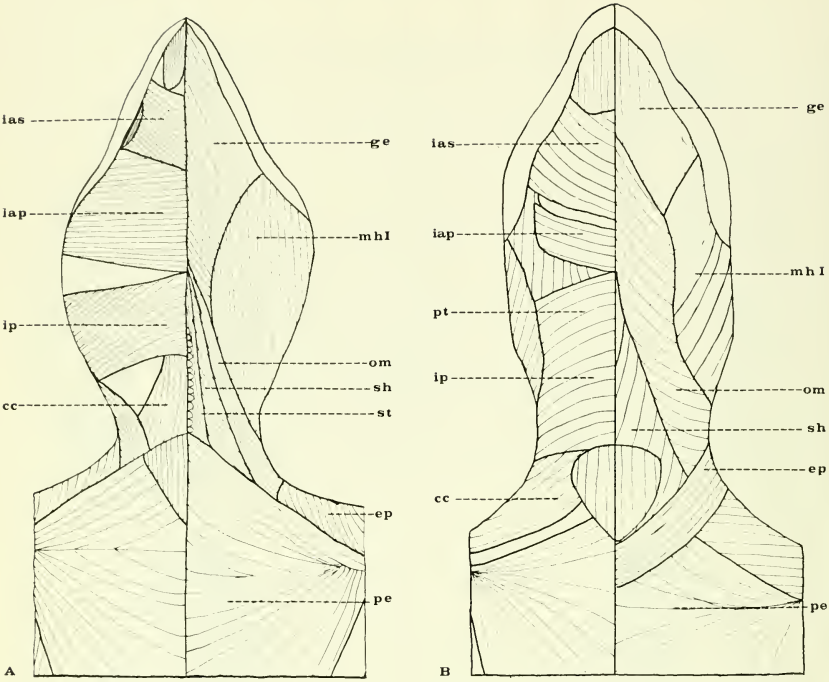
AR—Articular
CO—Coronoid
DE—Dentary
EC—Ectopterygoid
EP—Epipterygoid
FE—Fenestra exonarina
FR—Frontal

JU—Jugal
LA—Lacrimal
MX—Maxilla
NA—Nasal
OB—Orbit
PM—Premaxilla
PO—Postorbital

PRF—Prefrontal
PR—Parietal
PT—Pterygoid
PTF—Postfrontal
QU—Quadrate
SP—Splenial
SR—Surangular

Fig. 2. Lateral view of skull and medial view of mandible. A and C *Uta*, B and D *Urosaurus*.



CC—Constrictor colli
EP—Episternocleidomastoideus
GE—Genioglossus
IAP—Intermandibularis anterior profundus
IAS—Intermandibularis anterior superficialis
NP—Intermandibularis posterior
MHI—Mandibulohyoideus I
OM—Omohyoideus
PE—Pectoralis
SH—Sternohyoideus
ST—Sternothyroideus

Fig. 3. Ventral view of throat musculature; superficial depth at left and first depth at right. A. *Uta;* B. *Urosaurus.*

oid and the suture with the ectopterygoid. The ratio is *Urosaurus* .304 and *Uta* .354.

Ectopterygoid: Length (Figs. 1, 2) is between the suture with the pterygoid and the suture with the jugal and maxilla. The greatest diameter is at its point of union with the jugal and maxilla. The lower ratio is in *Uta* (.704) and the higher in *Urosaurus* (.753).

Vomers: Length (Fig. 1) is from the anterior suture with the premaxilla to the most posterior point of the suture with the palatine. Width is between the median border of the vomer at the ventral midline and the most lateral border where it attaches to the maxilla. The ratio in *Urosaurus* is .488 and in *Uta* .431. The vomers possess a small blunt projection which protrudes from its lateral border into the opening of the fenestra exochoanalis and fenestra vomeronasalis externa and divides the opening. This anterolateral projection is seen in both genera.

Palatine: Length is from the anterior suture with the vomer at the midline to the most posterior extension of the suture with the pterygoid (Fig. 1). Width is from the skull's midline to the lateral suture between the palatine and the maxilla. The ratio in *Urosaurus* is .848 and in *Uta* .579.

Premaxillae: Length (Figs. 1, 2) is from its anteroventral tip to its dorsal union with the nasal at the dorsal midline. Width is between the lateral sutures shared by the premaxillae with the maxilla on the ventral surface of the premaxilla. The ratio in *Uta* is .733 and in *Urosaurus* .656.

Maxillae: Length (Figs. 1, 2) is from the most anterior extension of the premaxillary process to the posterior-most extension of the maxillae where it sutured with the jugal and ectopterygoid. Width is the vertical distance from the ventral border of the maxillae to the dorsal-most extension at the point of suture with the nasals and prefrontals. The ratio in *Uta* is 3.96 and in *Urosaurus* .405.

Nasal: Length (Figs. 1, 2) is from the tip of the ventral border as it forms the fenestra exonarina to the posterodorsal extension that sutures with the prefrontal. Width is from its medial suture with its opposite member to its most lateral extension where it sutured with the maxilla and prefrontals. The ratio in *Urosaurus* is .410 and in *Uta* .332.

Prefrontal: Length (Fig. 1) is from the suture between the prefrontal and lacrimal bones at the anterior lip of the orbit, to the suture between the prefrontal and frontal. Width is from the suture between the prefrontal and lacrimals to the median point where the frontal, nasal, and prefrontal bones suture together. The ratio in *Uta* is .433 and in *Urosaurus* .419.

Lacrimal: Length is from the anterodorsal border as it sutures with the prefrontal and maxilla to the posterior border on the rim of the orbit as it sutures with the jugal (Fig. 2). Width is the distance between the dorsal border of the lacrimal at the rim of the orbit to its ventral border at its suture with the maxilla. The ratio in *Uta* is .101 and in *Urosaurus* .286.

Frontal: Length (Figs. 1, 2) is from the most anteromedian suture shared with the parietal. Width is between the most lateral posterior projections which suture with the parietal and postfrontal. The ratio in *Uta* is .903 and in *Urosaurus* .902.

Postfrontal: Length (Figs. 1, 2) is the extremities of its longest axis. Width is the distance between the parallel borders on the axis at right angles to the length. The ratio in *Urosaurus* is .255 and in *Uta* .288.

Jugal: Length (Figs. 1, 2) is between its most anterior projections as it sutures with the lacrimal and maxillae, to the posterior projection which sutures to the anteroventral border of the postorbital. Width is the distance between the two parallel borders at right angles to the length. The ratio in *Uta* is .092 and in *Urosaurus* .106.

Parietal: Two measurements (Figs. 1, 2) were taken. The anterior two-thirds of the bone was subjected to length-width measurements, with the length being the distance along the midline, from the anterior suture with the frontal to the suture between the parietal and the supraoccipital. Width is the distance between the two anterolateral projections that suture with the postorbital and postfrontal. The ratio in *Urosaurus* is .723 and in *Uta* .680.

Postorbital: Length (Figs. 1, 2) is between the anteroventral and postventral projections. Width is from the ventral border to the tip of the dorsal projection where it sutures with the parietal and postfrontal bones. The ratio in *Uta* is .711 and in *Urosaurus* .688.

Squamosal: Length (Fig. 1) is between the most anterior and posterior extremities. Width is between the parallel borders on an axis at right angles to the length. Ratio in *Urosaurus* is .370 and in *Uta* .325.

Quadrate: Length (Fig. 2) is from its dorsal border where it attaches to the squamosal and the ventral extremity of the condyle which articulates with the articular. Width is between its medial and lateral borders. The ratio in *Urosaurus* is .460 and in *Uta* .346.

Supratemporal fossa: Its length (Fig. 1) is the inside distance on the longest axis and width the inside distance on the longest axis at right angles to the length. The ratio in *Uta* is .467 and in *Urosaurus* .488.

Orbit: Length (Figs. 1, 2) is between the lacrimal and postorbital. Width is between jugal and frontal bones .The ratio (most circular opening) in *Urosaurus* is .806 and (most elliptical opening) in *Uta* .762.

Fenestra exonarina: Length (Fig. 1) is the internal distance between the lateral projection of the premaxilla and maxilla and the suture between the nasal and maxilla. Width is the inside distance between the lateral border of the premaxilla and the anterior border of the maxilla. The ratio (most circular opening) in *Uta* is .770 and (most elliptical opening) in *Urosaurus* .656.

The lower jaw consists of two paired rami united anteriorly in a mental symphysis. Each articulates posteriorly with the quadrate. The dentary of each ramus bears a single row of pleurodont teeth, whereas the remaining bones (articular, surangular, angular, splenial, and coronoid) are edentate.

Dentary: Length is from the anterior tip to the posterior-most projection on the lateral surface of the mandible (Fig. 2). Width is the vertical distance bewteen the top and the bottom of the mandible, immediately in front of the coronoid. The ratio in *Uta* is .163 and in *Urosaurus* .124.

Articular: Length (Fig. 2) is from it most anterior projection on the median surface where it sutured to the coronoid and splenial to the most posterior tip of the retroarticular process. Width is from the most ventromedial projection of the angular process to the opposite border of the articular where it sutured with the surangular on the lateral surface. The ratio in *Urosaurus* is .399 and in *Uta* .207.

The angular process of the articular bone differs in shape and size in each genus. This projection was also subjected to length-width measurements. The length is the greatest length of the mandible and was contrasted with the width of the articular, which in part is a result of the size of the angular process. *Urosaurus* .875 has the greatest ratio (shortest, widest) while the smallest (longest, narrowest) is in *Uta* .824.

Surangular: Length is the longest anterior-posterior axis on the lateral surface of the mandible (Fig. 2). Width is the longest dorsal-ventral axis in the area of the anterior sutures with the dentary and coronoid on the lateral surface. The ratio (shortest, widest) is in *Urosaurus* .271 and in *Uta* .185.

Spenial: Length is the longest anterior-posterior axis and the greater dorsal-ventral axis is the width. The ratio (shortest, widest) is in *Uta* .174 and in *Urosaurus* .156.

Angular: The angular is roughly fusiform; its length is between the most anterior and most posterior projections. Width is between the opposite borders on an axis at right angles to the length. The ratio (shortest, widest) in *Urosaurus* is .284 and in *Uta* .280.

Coronoid: Length is from the dorsal tip of the bone to the tip of the ventral-most projection on the lateral surface (Fig. 2). Width is between anterior and posterior borders where they contact the dorsolateral surface of the mandible. The ratio in *Urosaurus* is .591 and in *Uta* .560.

MYOLOGY

To avoid confusion, the terminology used for the following descriptions of the muscles is that of Robison and Tanner (1962), Jenkins and Tanner (1968), and Avery and Tanner (1954, 1971). The musculature also follows the basic iguanid pattern described by the above. Only deviations will be noted in the test.

Throat Musculature

M. Intermandibularis anterior superficialis is constant in both genera examined with the following exception: slightly broader in *Urosaurus* than *Uta* (Fig. 3). However, in both genera the muscle is sheetlike with the width at least half the length.

M. Intermandibularis anterior profundus is relatively consistent in its location; however, in *Uta* it is a wide band of muscle attached to the intermandibularis anterior superficialis. In *Urosaurus* it is a thin sheet separated anteriorly from the intermandibularis anterior superficialis and posteriorly from the intermandibularis posterior by a thin membrane (Fig. 3).

M. Intermandibularis posterior is continuous posteriorly with the constrictor colli from which it can be delineated by a natural separation of the muscle fiber bundles (Figs. 3, 9 and 10). The possession of this separation is varied in the genera examined. In *Urosaurus* the constrictor colli and intermandibularis posterior are closely associated along their entire common border. In *Uta* the two muscles are separated totally laterally but are continuous for a short distance near the midline raphe.

M. Mandibulohyoideus I in *Urosaurus* has approximately one-half of its body covered by the omohyoideus, whereas in the *Uta* only a small posterior portion is covered (Fig. 3).

M. Mandibulohyoideus II was described by Avery and Tanner (1971) for other iguanids. However, we were unable to locate this muscle in either *Uta* or *Urosaurus*.

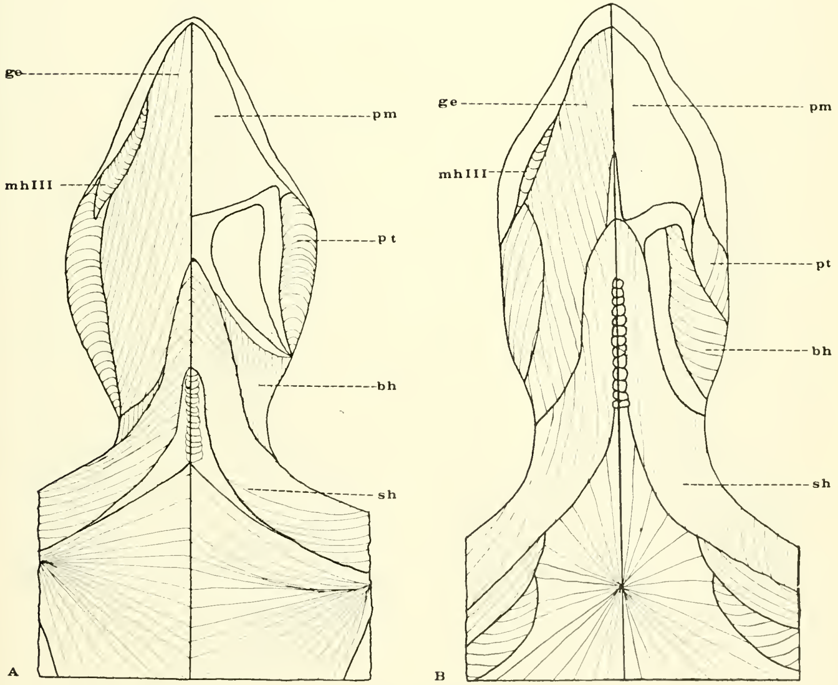
M. Mandibulohyoideus III in both *Uta* and *Urosaurus* arises from the ventromedial surfaces of the dentary and angular between the anterior and posterior myohoid foramina (Fig. 4). The narrow insertion is on the lateral surface of the ceratohyal distal to its midpoint.

M. Genioglossus is a thick bandlike muscle in both genera which occupies a large area between the mandibular rami (Figs. 3 and 4). Its position is ventral to the tongue and anterior to the basihyal. The first, second, and third mandibulohyoideus and the intermandibularis muscles are all dorsal to it.

M. Hyoglossus is as described in other iguanids.

M. Branchiohyoideus in *Uta* (as in *Sauromalus*) has a narrow insertion on the first ceratobranchial, whereas in *Urosaurus* the insertion covers over half the distal portion of the first ceratobranchial (Fig. 4).

M. sternohyoideus, as reported in the literature, is subject to considerable confusion concerning its limits (Figs. 3, 4, 6). Davis (1934:19) considers the superficial layer to be divisible into three parts in *Crotaphytus*. One of these muscles he calls the omohyoideus. Robison and Tanner (1962:6) consider this muscle continuous in the same genus. Oelrich (1956:51-52) treats this muscle in *Ctenosaura* as being continuous, but owing to the different origin and direction of the fibers he separates the layers into omohyoideus and sternohyoideus. Kesteven (1944:245-246) studied the agamid, *Physignathus*, suggesting a separation in young specimens and treats these layers as con-



BH—Branchiohyoideus
GE—Genioglossus
MHIII—Mandibulohyoideus III
PM—Pharyngeal membrane
PT—Pterygoidmandibularis
SH—Sternohyoideus

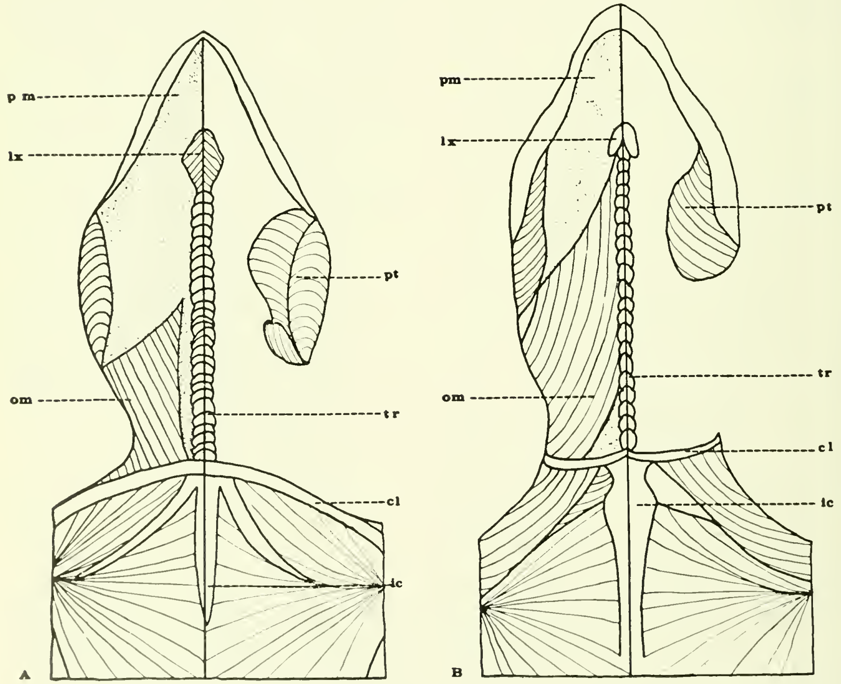
Fig. 4. Ventral view of throat musculature; second depth at left and third depth at right. A. *Uta;* B. *Urosaurus.*

sisting of three parts which he considers to represent the similar, though distinct, divisions present in *Varanus*. In the iguanines Avery and Tanner (1971) treated the sternohyoideus complex as three separate muscles, sternohyoideus, sternothroideus, and omohyoideus. This arrangement is followed here. In both genera examined, the sternohyoideus forms a broad elongated sheet of muscle covering the posterior portion of the mandibulohyoideus I muscle.

M. omohyoideus is sheetlike and forms the lateral extension of the sternohyoideus complex (Figs. 3, 5, 10). In both genera it originates medially from the lateral tip of the transverse process of the interclavicle with some fibers of the episternocleidomastodeus. Laterally, the omohyoideus originates from the anterolateral surface of the clavicle and anterior border of the suprascapula. Its fibers pass obliquely anterior to insert on the posterior margin of the first ceratobranchial and the proximal end of the second ceratobranchial cartilages.

In both genera the median border is separated from the lateral border of the sternohyoideus. The delineation of both muscles must be made by comparing the origins and insertions. In *Urosaurus* it is easily separated, as the fibers of this muscle pass oblique to those of the sternohyoideus covering most of the mandibulohyoideus I. In *Uta* it is a thin band just lateral to the sternohyoideus.

M. Sternothyroideus is the most medial extension of the sternohyoideus complex



CL	Clavicle	OM	Omohyoideus	TR	Trachea
IC	Interclavicle	PM	Pharyngeal membrane		
LX	Larynx	PT	Pterygoidmandibularis		

Fig. 5. Ventral view of throat musculature: fourth depth at left and fifth depth at right. A. *Uta*; B. *Urosaurus*.

and can be separated from the other members of the group by its different origin and insertion (Fig. 3). The name sternothyroideus is used as in Camp (1923: 451), who figured it as the deep member of the complex in *Brachylophus*.

The origin is considered to be those fibers arising from the interclavicle and sternum. These fibers pass anteriorly and parallel to the trachea to insert on the hyoid at the point of union between the basihyoid and hypohyal.

In *Urosaurus* the lateral border of the sternothyroideus and the median border of the sternohyoideus are difficult to determine. In *Uta* their separation is distinguishable since the three muscles have fibers oblique to one another as described for *Sauromalus* by Avery and Tanner (1971).

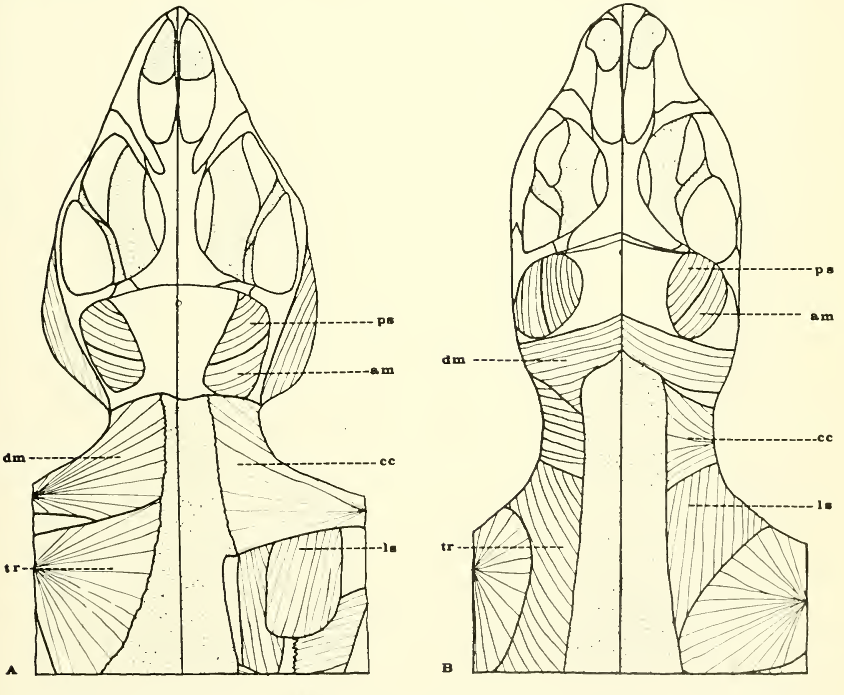
Neck Musculature

M. Constrictor colli is variable in width inboth genera (Figs. 3, 4, 9). It is widest, covering most of the lateral surface of the neck, in *Urosaurus*. A narrow constrictor colli occurs in *Uta*.

M. Episternocleidomastoideus was found as a thin band of muscle extending over the shoulder in *Uta*, whereas in *Urosaurus* it is at a greater depth (Figs. 3, 7, 9, 10, and 11).

M. Depressor mandibularis (Figs. 6, 9, 10) is divided into three bundles as described by Avery and Tanner (1971). The third bundle (cervicomandibularis) in *Uta* and *Urosaurus* is completely obscured by the more superficial constrictor colli.

M. Levator scapulae superficialis is not



AM—Adductor mandibularis externus medius
CC—Constrictor colli
DM—Depressor mandibularis
LS—Levator scapulae superficialis
PS—Pseudotemporalis superficialis
TR—Trapezius

Fig. 6. Dorsal view of head and neck musculature: superficial depth at left and first depth at right. A. *Uta*; B. *Urosaurus*.

as fan shaped in *Uta* as in *Urosaurus* (Figs. 6, 7, 10 ,11, and 12).

M. Levator scapulae profundus has a more superficial position in *Uta* than in *Urosaurus* (Figs. 7, 12).

Temporal Musculature

M. Pterygomandibularis does not deviate from the typical iguanid pattern (Figs. 4, 5).

M. Levator angularis oris differs in size in *Urosaurus* where it covers over half the intratemporal fossa (Fig. 9). In *Uta* it is narrower, covering approximately one-third of the fossa.

M. Adductor mandibularis externus superficialis is similar to that of other iguanids (Figs. 9, 10).

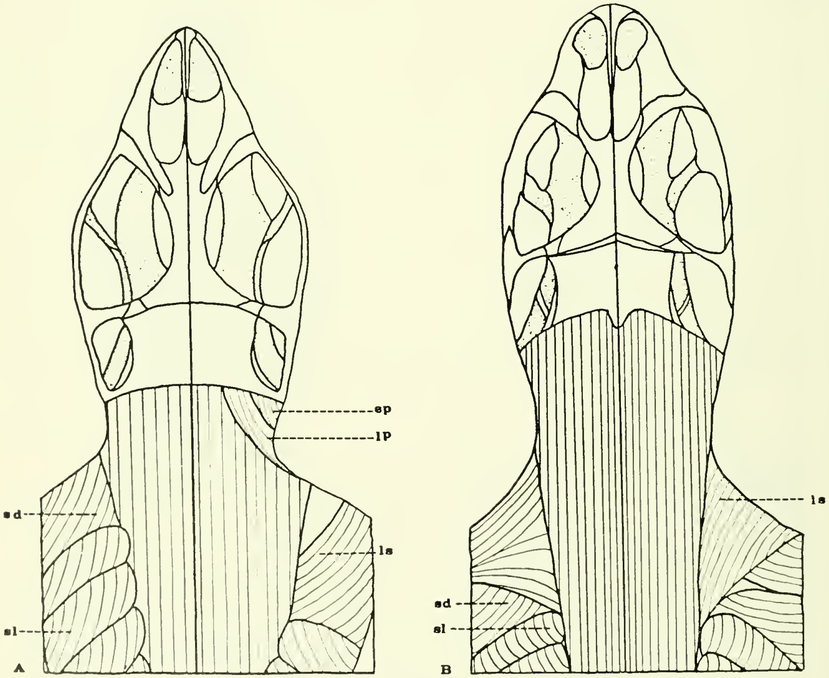
M. Adductor mandibularis externus medius is also with the typical iguanid pattern (Figs. 6, 9, 10, 11).

M. Adductor mandibularis externus profundus is as in other iguanids (Fig. 12).

M. Pseudotemporalis superficialis does not deviate from other iguanids (Figs. 6, 12).

M. Pseudotemporalis profundus is more obscured by the levator pterygoideus in *Urosaurus* than in *Uta* (Fig. 13).

M. Adductor mandibularis posterior shows some variations in the two genera, particularly in the location of the muscle with reference to the auditory meatus (Fig. 13). In *Urosaurus* it is located both ventral and anterior to the meatus, whereas in *Uta* the muscle is found slightly ventral to the meatus.



EP—Episternocleidomastoideus
LP—Levator scapulae profundus
LS—Levator scapulae superficialis
SD—Serratus (dorsal part)
SL—Sacrolumbalis

Fig. 7. Dorsal view of head and neck musculature: second depth at left and third depth at right. A. *Uta*; B. *Urosaurus*.

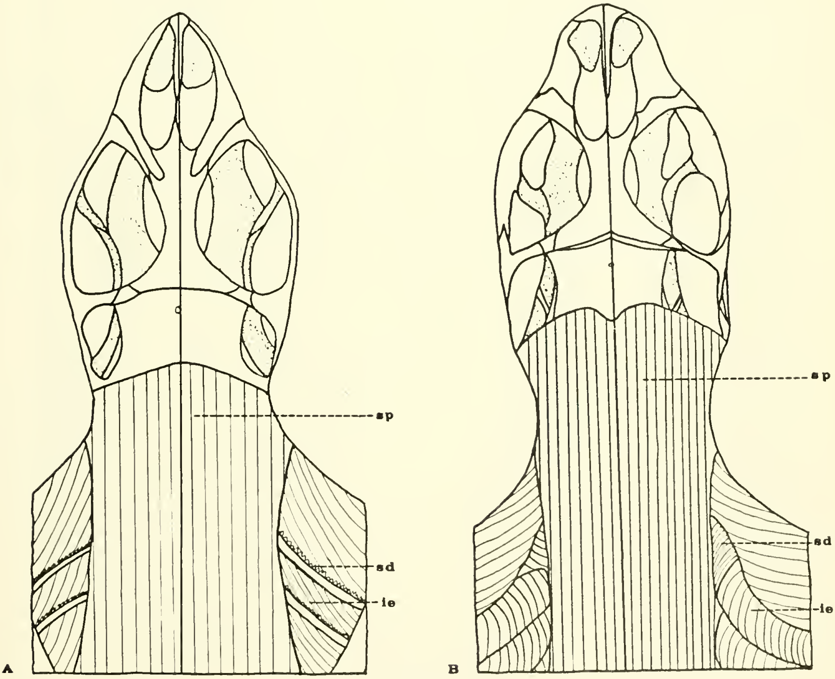
M. Levator pterygoideus is as seen in other iguanids (Fig. 14).

M. Protractor pterygoideus has a much larger insertion on the medial crest of the quadrate in *Urosaurus* than in *Uta* (Figs. 13, 14).

Discussion

A study of the anterior osteology and myology of *Uta* and *Urosaurus* reveals some distinct anatomical differences between the two genera.

Mittleman (1942) considered the relationship between *Uta*, *Urosaurus*, and the iguanines (*Sauromalus*, *Dipsosaurus*, and *Ctenorsaura*). He regarded *Uta* and *Urosaurus* as distinct genera. Savage (1958) outlined the iguanine characteristics and included *Crotaphytus* in that evolutionary line. He also determined some structural differences between *Uta* and *Urosaurus*. The differences cited by Savage include *Urosaurus* possessing a pectoral girdle of the urosaurine type: lateral xiphisternal ribs present and no supranasal scales. *Uta* is distinctly different in having a pectoral girdle of the utiform type, no lateral xiphisternal ribs, and supranasal scales separating nasals from internasals. Avery and Tanner (1964) present several myological differences between *Sauromalus* and *Crotaphytus* and indicate these two genera are not in the same evolutionary line, indicating that at least two major subdivisions exist in the family Iguanidae. Etheridge, in 1964, also examined the iguanines and separated *Crotaphytus* from them based on osteological differences. He states that osteological comparison suggests that three subgroups of sceloporines may exist: (1) *Holbrookia*, *Callisaurus*, and *Uma* possessing the scapular fenestra; (2) *Uta*, *Urosaurus*, *Sator*, and *Sceloporus* demonstrating the absence of the scapular



IE—Intercostalis externi SD—Serratus (dorsal part) SP—Spinus dorsi

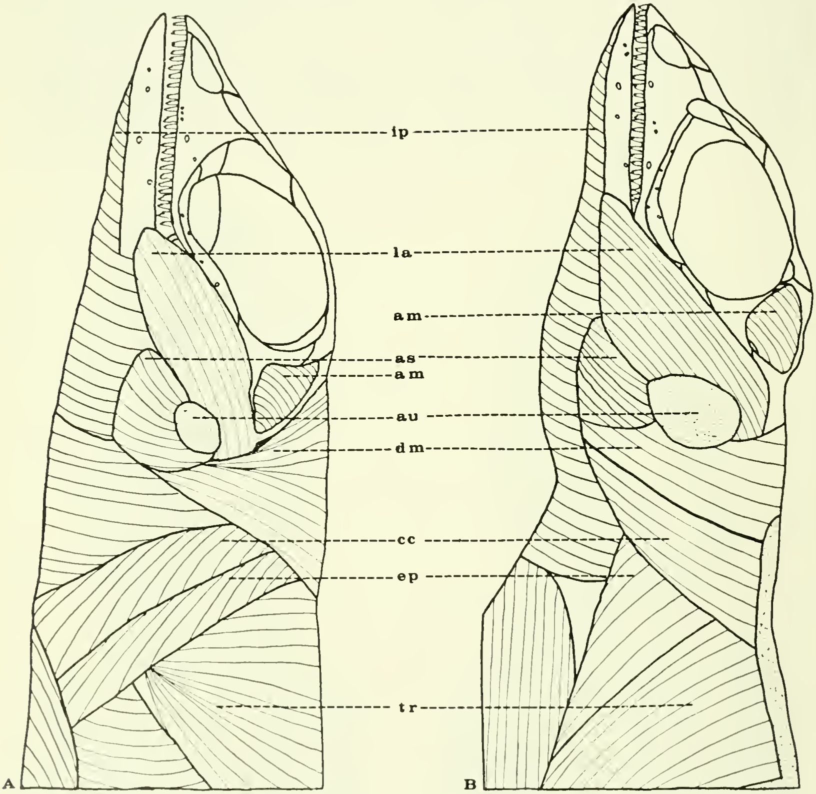
Fig. 8. Dorsal view of head and neck musculature; fourth depth at left and fifth depth at right. A. *Uta*; B. *Urosaurus*.

fenestra; and (3) *Petrosaurus* possessing very few osteological comparisons to the other sceloporines.

Presch (1969) reported that the osteological chararteristics indicate that the horned lizards (*Phrynosoma*) form a highly specialized genus within the sceloporine group of genera. *Phrynosoma* is distinguished from all other members in having a large sternal fontanelle. *Petrosaurus*, he states, is clearly primitive with its moderately sized sternal fontanelle and four sternal ribs. Of the two groups derived from *Petrosaurus*, the least altered are *Urosaurus*, *Uta*, *Sceloporus*, and *Sator*, with hooks on the clavicle and a covering over the anterolateral processes of the frontal. Thus Presch places *Uta* and *Urosaurus* in the same group but as distinct genera.

Zug (1971) studied arterial patterns in many iguanids and found differences between *Uta* and *Urosaurus*. In his Figures 10 and 15 he illustrates these differences. Particularly significant is the representation of separate phylogenetic lines for these genera.

Recently Purdue and Carpenter (1972)

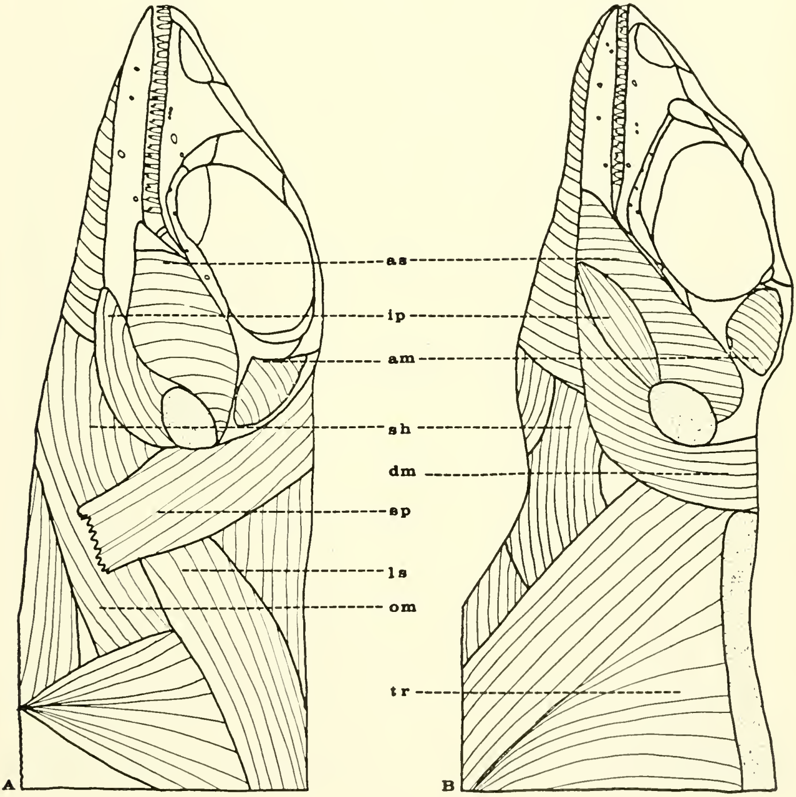


AM—Adductor mandibularis externus medius
AS—Adductor mandibularis externus superficialis
AU—Auditory meatus
CC—Constrictor colli
DM—Depressor mandibularis
EP—Episternocleidomatoideus
IP—Intermandibularis posterior
LA—Levator angularis oris
TR—Trapezius

Fig. 9. Lateral view of head and neck musculature; superficial depth. A. *Uta*; B. *Urosaurus*.

have studied the relationships of *Sceloporus*, *Uta*, and *Urosaurus* as determined by their display motions and based on ratios of hip and shoulder movement to vertical eye movement. They suggest that *Uta* and *Urosaurus* are distinct genera and that *Urosaurus* is derived from one group of *Sceloporus*, while *Uta* is more closely related to *Petrosaurus*.

Larsen and Tanner (1975) have presented a new phylogeny for the sceloporines based on external characteristics including the development of specialized scales and structure of the gular fold, and internal characters including hip and shoulder ratios. They indicate that *Sceloporus* is advanced and derived from one line of sceloporines, including *Sator*, *Urosaurus*, *Uta*, and *Petrosaurus*; while *Phrynosoma* and the sand lizards, including *Uma*, *Callisaurus*, *Holbrookia*, and *Cophosaurus*, comprise a separate line of evolution. They separate the primitive species of *Sceloporus* from that genus and resurrect Cope's genus *Lysoptychus* for them. They also consider *Uta* and *Urosaurus* to be closely related, with *Uta* being the more primitive.



AM—Adductor mandibularis externus medius
AS—Adductor mandibularis externus superficialis
DM—Depressor mandibularis
EP—Episternocleidomastoideus
IP—Intermandibularis posterior
LS—Levator scapulae superficialis
OM—Omohyoideus
SH—Sternohyoideus

Fig. 10. Lateral view of head and neck musculature: first depth. A. *Uta*; B. *Urosaurus*.

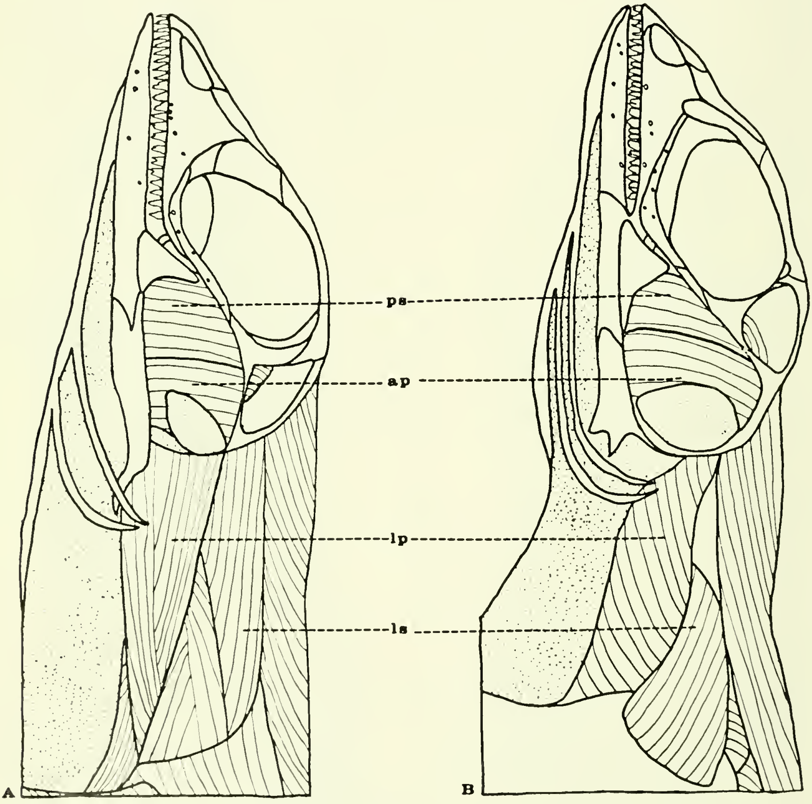
Osteology

As stated earlier, length-width measurements of bones and bone shapes were utilized to analyze the osteological relationships between the two genera. The ratio means in Tables 1 and 2 were used to make these relationships clear. Utilizing the method of Avery and Tanner (1971), one can assume that a difference of .40 or fewer percentage points (.20-.60) between means of the same bone indicates a close relationship. The possession of bones with similar shape is also an indicator of close relationship.

Based on comparisons of the skulls of iguanine lizards, Avery and Tanner (1971) indicate osteological characters of the skulls of iguanid lizards to be stable within generic limits. This osteological stability is also demonstrated by the skulls of *Uta* and *Urosaurus*.

Reviewing Tables 1 and 2, the 35 characteristics and corresponding mean ratios indicate 24 structures with mean ratios differing by .40 or more percentage points (.20-.65).

As indicated by Etheridge (1964), the difference between the skull length and



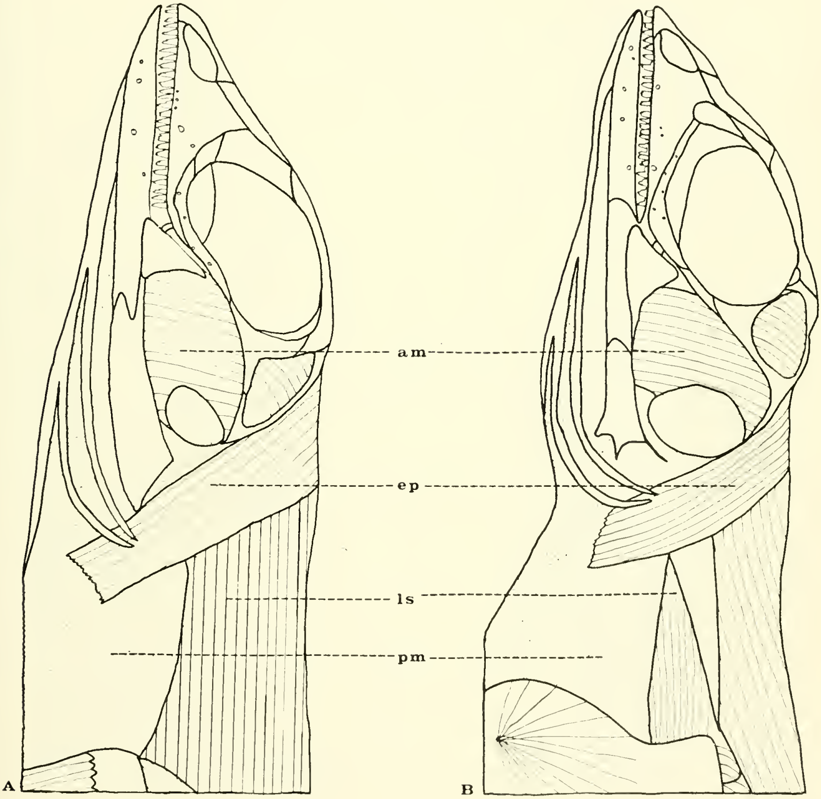
AP—Adductor mandibularis externus profundus
LP—Levator scapulae profundus
LS—Levator scapulae superficialis
PS—Pseudotemporalis superficialis

Fig. 11. Lateral view of head and neck musculature; second depth. A. *Uta;* B. *Urosaurus.*

width ratio in *Uta* and *Urosaurus* is almost negligible. However, our measurements of the basisphenoid and basioccipital bones show differences of 1.05 and 1.46 points respectively, along with the more posterior location of the suture between the two structures.

Considering the ventral bone structures (Fig. 1), the follwoing mathematical differences exist. Both the pterygoid and ectopterygoid bones differ by more than .40 points (Tables 1 and 2); however, the ectopterygoid possessed by *Urosaurus* shows anterior wings extending to the maxilla, not seen in *Uta*. The primary differences found between the vomer and palatine bones in both genera is mainly the positioning of their common suture. In *Urosaurus* the suture extends anteromedially from the inferior orbital foramen to the fenestra exochioanalis, whereas in *Uta* the suture is found extending laterally from the anterior portion of the pyriform recess to the maxilla.

In reference to the nasal capsule (nasal, prefrontal, lacrimal, and septomaxilla), there are found ratio differences in the nasal and lacrimal (slight difference in the prefrontal) and practically no structural peculiarities. The premaxilla and



AM—Adductor mandibularis externus medius
EP—Episternocleidomastoideus
LS—Levator scapulae superficialis
PM—Pharyngeal membrane

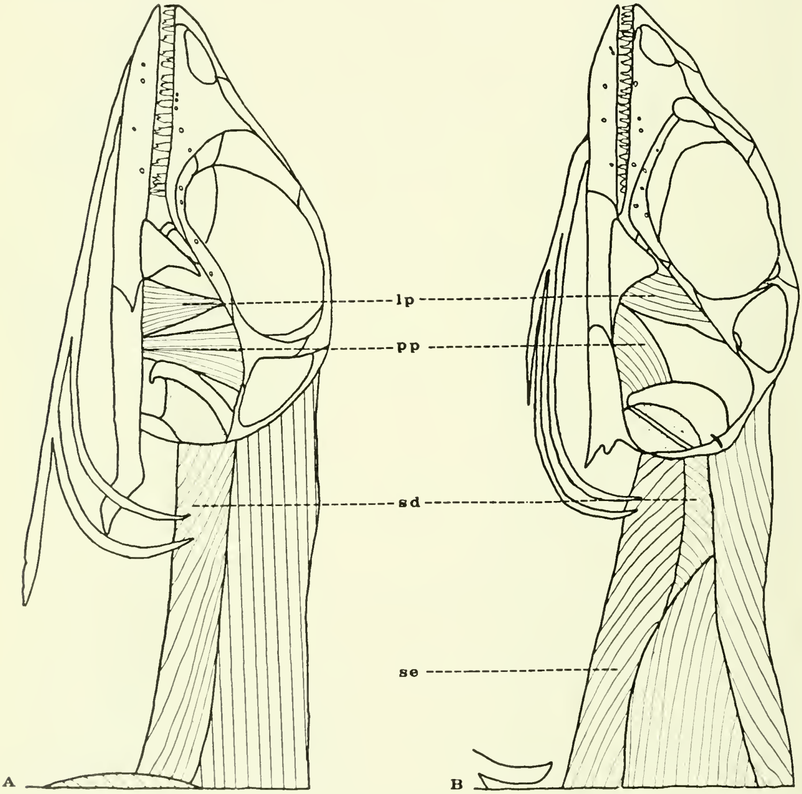
Fig. 12. Lateral view of head and neck musculature; third depth. A. *Uta;* B. *Urosaurus.*

maxilla of the palate complex show a discrepancy only in the premaxilla. The premaxillary bones of the two genera differ by .77 points with the premaxilla of *Uta* being narrower anteriorly than in *Urosaurus*.

The parietal, squamosal, and quadrate (of the temporal fenestra portion of the maxillary segment) all differ in size, shape, and ratio. The parietal in *Uta* is much more rectangular and broad than in *Urosaurus* and covers more of the posterior portion of the braincase. The difference between the squamosal and quadrate in both genera is mostly in ratio (shape-size) rather than in location.

On the dorsal area of the skull a striking difference is noticed in the size and shape of the fenestra exonarina. In *Uta* the fenestra is oval and quite similar to that of *Sauromalus o. multiforaminatus* (Avery and Tanner, 1964), whereas in *Urosaurus* the anterior portion of the fenestra is expanded anterolaterally.

Turning to the mandible, we see several differences. The articular differs by 1.92 points in *Uta* and is only half the length seen in *Urosaurus*. The largest mandib-



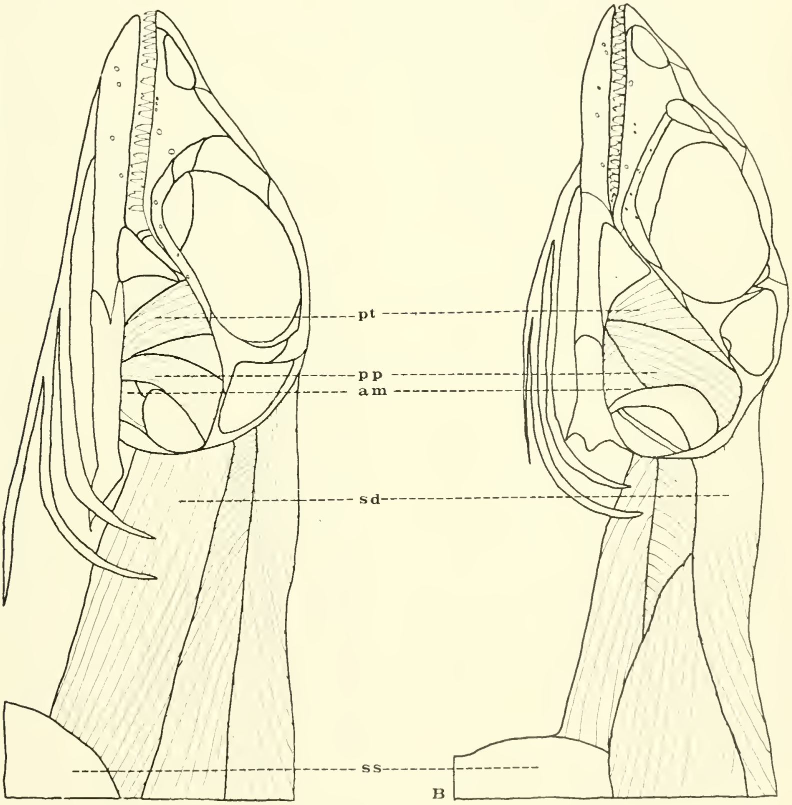
AM—Adductor mandibularis posterior
PP—Protractor pterygoideus
PT—Pseudotemporalis profundus
SD—Spinus dorsi
SS—Suprascapula

Fig. 13. Lateral depth of head and neck musculature; fourth depth. A. *Uta*; B. *Urosaurus*.

ular difference is in the size and location of the surangular, where the ratio differential is .86 points and the position in *Urosaurus* is directly ventral to the coronoid. In *Uta*, however, it is posteroventral to the coronoid with only an anterior wing making contact with the coronoid anteriorly. This arrangement of the surangular and coronoid found in *Uta* is similar to *Amblyrhynchus cristatus*, *Brachylophus faciatus*, *Chalarodon madagascarensis*, *Conolophus pallidus*, *Ctenosaura pectinata*, *Cyclura macleyi*, *Dipsosaurus dorsalis*, *Iguana iguana*, *Oplurus sebae*, and *Sauromalus obesus* (Avery and Tanner, 1971). None of these are similar to *Urosaurus*.

Myology

The anterior anatomy in *Uta* when compared with that in *Urosaurus* shows observable myological differences. In considering the M. omohyoideus, M. sternohyoideus, and M. sternothroideus, one can see that all three muscles were distinctly separated in *Uta* as they were reported for the iguanids *Cyclura nuchalis* and *Sauromalus obesus* by Avery and Tanner (1971), whereas *Urosaurus* resembles slightly that of *Brachylophus fasciatus*.



LP—Levator pterygoideus
PP—Protractor pterygoideus
SD—Spinus dorsi
SE—Serratus (dorsal part)

Fig. 14. Lateral view of head and neck musculature; fifth depth. A. *Uta*; B. *Urosaurus*.

The dorsal musculature at the first depth shows a distinct difference between *Uta* and *Urosaurus*. The M. levator scapulae superficialis, which is evident in all species studied by Avery and Tanner (1971) as well as in *Uta*, was overlaid by the trapezius complex in *Urosaurus*. Another distinction of the ventral musculature is that seen in the M. episternocleidomastoideus. In *Uta*, as in the genera studied by Avery and Tanner, the M. episternocleidomastoideus and the levator scapulae profundus are found anterior to the M. levator scapulae superficialis, whereas in *Urosaurus* the position of these two muscles is posterior to M. levator scapulae superficialis.

Lateral musculature shows some similarities between *Urosaurus*, *Chalarodon madagascarensis*, and *Oplurus sebae*, while the similarity of *Uta* to *Sauromalus obesus* and *Cyclura nuchalis* (Avery and Tanner 1971) is noticeable. In *Urosaurus* the M. episternocleidomastoideus is overlaid by the trapezius, whereas in *Uta* it is not covered. The M. episternocleidomastoideus and M. levator scapulae superficialis of *Urosaurus* are buried beneath the second depth of muscle tissue, while in *Uta* these muscles are mostly superficial.

The orientation of the M. levator scapulae superficialis and M. levator scapulae profundus at the third depth is the same in *Urosaurus* and *Chalarodon madagascarensis*, while these muscles in *Uta* resemble *Sauromalus obesus* and *Cyclura nuchalis*. In *Urosaurus* the M. levator scapulae superficialis covers the M. levator scapulae profundus posteriorly as seen in *Chalarodon madagascarensis* (Avery and Tanner, 1971). In *Sauromalus obesus* the common border of the M. levator scapulae profundus and M. levator scapulae superficialis is similar to that in *Uta*.

The temporal musculature of *Cyclura nuchalis* (Avery and Tanner, 1971), M. protractor pterygoideus, M. pseudotemporalis profundus, and M. levator pterygoideus appears to be similar to that of *Uta*, whereas in *Urosaurus* these muscles are seemingly very similar to those of *Chalarodon*.

Phylogenetic Relationships

Larsen and Tanner (1975) consider *Uta* to be more primitive than *Urosaurus* and both more primitive than *Sceloporus*, based on internal and external characters. We agree with this analysis of *Uta's* relationship to *Urosaurus*. We believe that *Uta* is more primitive for the following reasons: 1. The ectopterygoid of *Uta* is simple in structure and shape, while that of *Urosaurus* is greatly expanded and more complex in shape. 2. The fenestra exonarina of *Uta* is similar to that of *Sauromalus*, a primitive iguanine lizard. 3. The structure of the surangular and coronoid bones in *Uta* is similar to that seen in the more primitive iguanines and the Madagascar iquanids. 4. The omohyoideus muscle complex in *Uta* may be subdivided into three distinct muscle bundles as seen in the primitive *Cyclura* and *Sauromalus*, wheras *Urosaurus* resembles the omohyoideus configuration seen in the specialized *Brachylophus*. 5. In *Uta* the levator scapulae superficialis, levator scapulae profundus, and the episternocleidomastoideus muscles have a configuration similar to the more primitive iguanines. In *Urosaurus* the muscle pattern shows considerable deviation. 6. In *Uta* the levator scapulae superficialis is superficial while it is overlain by the trapezius complex in *Urosaurus*, indicating to us a higher degree of specialization.

The similarity of these two genera to the Madagascar iguanids *Chalarodon* and *Oplurus* remains a confused question. If *Oplurus* is ancestral to the iguanine lizards as indicated by Avery and Tanner (1971), is *Chalarodon* also ancestral to the sceloporine lizards? Apparently not since both *Uta* and *Urosaurus* share some characteristics with *Chalarodon* and *Oplurus* without establishing a consistent pattern of relationship. These similarities are more likely the result of parallelism than a close phylogenetic relationship. All four genera are desert animals and *Chalarodon* superficially resembles both *Uta* and *Urosaurus* externally.

Perhaps future comparisons should be made between Phrynosoma and *Petrosaurus* and the Madagascar iguanids to determine the phylogenies of the main lines of iguanid evolution and the Madagascar iguanids.

CONCLUSIONS AND SUMMARY

Data derived from the preceding observations strongly indicate that *Uta* and *Urosaurus* are distinct genera. These conclusions are based on the distinct osteological and myological characteristics found in the head and throat anatomy.

Osteological differences are summarized as follows: 1. Bones showing major differences in size and shape are the basisphenoid, basioccipital, pterygoid, ectopterygoid, premaxilla, articular, and surangular. 2. The ectopterygoid possesses an extended anterior wing to the maxilla in *Urosaurus* which is not present in *Uta*. 3. The parietal in *Uta* is much more rectangular and broader than in *Urosaurus*. 4. The fenestra exonarina in *Uta* is oval, whereas in *Urosaurus* the anterior portion is expanded anterolaterally. 5. The position of the surangular in *Urosaurus* is directly ventral to the coronoid, but in *Uta* it is posteroventral to the coronoid with only an anterior wing making a narrow contact with the coronoid.

Several noticeable generic myological differences are apparent: 1. A distinct separation of the M. omohyoideus, M. sternohyoideus, and M. sternothryoideus is seen in *Uta*, whereas in *Urosaurus* only the M. omohyoideus and M. sternohyoideus are discernible. 2. The M. levator scapulae superficialis at the first depth is superficial in *Uta* but is overlain by the trapezius complex in *Urosaurus*. 3. In *Uta* the M. episternocleidomastoideus and the M. levator scapulae profundus are anterior to the M. levator scapulae superficialis, whereas in *Urosaurus* the position of the first two muscles is posterior to the latter muscle. 4. The M. protractor pterygoideus, M. pseudotemporalis profundus, and M. levator pterygoideus of *Uta* are similar to those of *Cyclura nuchalis*, while in *Urosaurus* these muscles are similar to *Chalarodon*.

Because *Uta* and *Urosaurus* exhibit such distinct anatomical differences, the separate generic designations assigned to them are considered to be valid. Phylogenetically *Uta* is considered to be older and more primitive than *Urosaurus* because of (1) the simple structure of the ectopterygoid in *Uta*, (2) the primitive shape of the fenestra exonarina, (3) the common arrangement of the surangular and coronoid bones in *Uta*, (4) the common arrangement of the M. omohyoideus complex in *Uta* and the primitive iguanines, and (5) the common configuration of the posterior skull and anterior shoulder musculature of *Uta* and the primitive iguanines.

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DISTRIBUTION AND ABUNDANCE OF THE BLACK-BILLED MAGPIE (*PICA PICA*) IN NORTH AMERICA

Carl E. Bock[1] and Larry W. Lepthien[1]

ABSTRACT.— Analysis of Audubon Society Christmas bird count data and certain environmental variables shows the degree to which the Black-billed Magpie is a bird of cool arid regions in North America. The abundance and distribution of this species appear to be limited by two major climatic barriers: increasing summer temperatures in the Southwest and increasing summer humidity and precipitation on the central plains.

The Black-billed Magpie (*Pica pica*) is one of the most conspicuous passerine birds on the western plains and in the Great Basin. In this paper we are concerned with what factors determine the abundance pattern and southern and eastern limits of distribution in this species. Linsdale (*in* Bent 1946:134) noted that "a rather striking relation to climate exhibited by this bird has not been clearly explained" or, specifically, that *Pica pica* in the New World seems restricted to the "cold type steppe dry climate" region characteristic of that portion of the United States north of approximately 35° latitude, west of about 100° longitude, and east of the Sierra Nevada-Cascade Range. Within this area *Pica pica* is widely distributed, breeding at most elevations up to 10,500 ft. (Ligon, 1961).

The one universal characteristic of magpie habitat is an association of thickets or riparian areas, necessary for breeding and roosting, with open meadows, grassland, or sagebrush fields suitable for its method of foraging (Linsdale, 1937; Gabrielson and Jewett, 1940; Grinnell and Miller, 1944; Jones, 1960; Erpino, 1968). Without doubt these habitat requirements explain the absence of magpies from the closed boreal forests in the north. However, this sort of habitat mosaic occurs along watercourses in the Great Plains and Southwest, so that it is not immediately apparent why this species does not occupy a larger part of the United States.

We have analyzed the winter abundance pattern of *Pica pica* using data from the annual Audubon Society Christmas bird counts. Although magpies may wander somewhat in winter (Jewett et al., 1953), the bulk of the population seems to stay within the breeding range. Christmas count data were compared with certain climatic variables taken from maps of 50-year climatic means published by the U.S. Department of Agriculture (1941). Results provide insight into those environmental factors which directly or indirectly influence the abundance and distribution of the Black-billed Magpie.

Methods

Each Christmas count is a standardized one-day census conducted inside a prescribed circle 15 miles in diameter. Hundreds of such counts are made annually in North America. Data gathered include the number of each species seen and the number of "party-hours" of fieldwork as a measure of census effort. Published results of the counts provide an index to continent-wide patterns of bird distribution and abundance (Bock and Lepthien, 1974; Bystrak, 1974).

Details of techniques for computerized data storage, retrieval, and analysis have been described previously (Bock and Lepthien, 1974). In this case we retrieved data from the 1969-70, 1970-71, and 1971-72 Christmas counts (2,743 individual censuses), sorted these by blocks of five degrees of latitude and longitude, and computed mean number of birds per party-hour for all counts within each block (Fig. 1). Similar maps of climatic data were constructed for all latitude-longitude blocks at least partially within the United States, adapted from the maps in the U.S. Department of Agriculture (1941).

The statistics program BMD-02R (Dixon, 1971) was used to compute stepwise regression of magpie numbers against the series of climatic variables mapped.

Results

Figure 1 shows the winter abundance pattern of the Black-billed Magpie. Christ-

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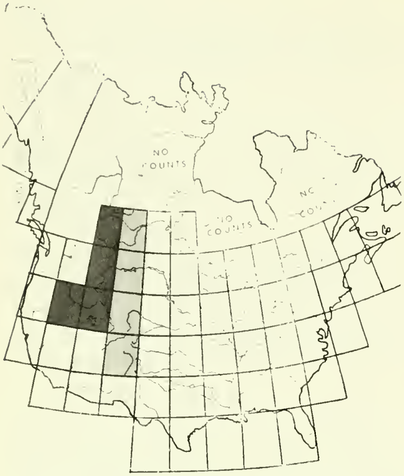

Fig. 1. Winter abundance pattern of the Black-billed Magpie, based on Christmas count data. Open blocks = no birds observed; four degrees of shading represent ≥ 5.0, 3.0-4.9, 1.0-2.9, and < 1.0 birds per party-hour, respectively.

Table 1. Correlation coefficients between Black-billed Magpie abundance and certain environmental variables. Bird data are from 1969-70, 1970-71, and 1971-72 Christmas counts, grouped by blocks of latitude and longitude (see Fig. 1); environmental data are 50-year means from USDA (1941).

Variable	All blocks (n = 47)	Correlation coefficient Blocks within or adjacent to magpie range (n = 26)
$\bar{X}$ annual temp	–.38*	–.41*
Maximum temp	–.20	–.40*
Minimum temp	–.39*	–.36
No. frost-free days	–.43*	–.51*
Annual precipitation	–.45*	–.33
Summer precipitation	–.45*	–.31
Winter precipitation	–.24	–.12
$\bar{X}$ July humidity	–.59*	–.50*

* $p < .05$

mas count data indicate that this species is restricted to the region described by Linsdale (1937) but that it is not uniformly distributed within that area. Highest densities were found in the northern Great Basin and on the northwestern plains of Montana, Alberta, and Saskatchewan. Densities appeared lower in the southern and eastern portions of the range.

Figure 1 suggests that those same factors limiting the distribution of the Black-billed Magpie also may be influencing its abundance within that range. Table 1 shows correlation coefficients between bird abundance and various climatic factors. It is evident that magpie densities are negatively correlated with a variety of temperature and moisture variables, whether or not one includes blocks outside the range of the species.

Tables 2 and 3 show the results of stepwise multiple regression of magpies and the climatic variables listed in Table 1. When data for all latitude-longitude blocks are used, only two variables (July humidity and maximum temperature) made a meaningful contribution to the regression equation, but these accounted for 54 percent of the variation in magpie abundance. Restricting the analysis to the species' range resulted in a stepwise regression including four independent variables and accounting for 59 percent of the pattern of magpie density (Table 3). Frost-free days entered as the best predictor (negative) within the range. This, however, is simply another parameter of temperature regime. Table 3 shows that the same family of variables is involved within the species range—namely, an inverse relationship to temperature and moisture during the warm season of the year.

Table 2. Stepwise multiple regression of eight environmental variables against winter abundance of Black-billed Magpies. Based upon Christmas count data and climate variables for 47 latitude-longitude blocks in the United States (see text and Fig. 1).

Step no.	Variable entered	R*	R^2**
1	July humidity	0.59	0.35
2	Maximum temperature	0.74	0.54

R* = multiple correlation coefficient
R^2** = coefficient of determination, equivalent to percent of variation in magpie abundance explained at each step

Table 3. Same as Table 2, except based only upon 26 latitude-longitude blocks in the United States within or adjacent to Black-billed Magpie range (see Fig. 1).

Step no.	Variable entered	R	R^2
1	No. frost-free days	0.51	0.26
2	July humidity	0.71	0.51
3	Summer precipitation	0.75	0.56
4	Maximum temperature	0.77	0.59

DISCUSSION AND CONCLUSIONS

Results of this study show the degree to which the Black-billed Magpie is a bird of cool arid climates in the United States. This does not necessarily mean that magpie distribution and abundance actually are determined by climate, or even by the influence of climate on food. It could be that the species is restricted by habitat availability or by the appearance of close competitors coincidental with changes in climatic regime. We can provide no definitive answer to this dilemma, but a few considered speculations are in order, particularly as they might stimulate more research.

First, there is no clear break in suitable habitat in the United States which should limit magpie distribution, except in the West where the closed coniferous forests constitute a sharp boundary. Riparian habitat along such watercourses as the Rio Grande and the North Platte, South Platte, Arkansas, and Colorado rivers all support Black-billed Magpie populations; yet, *Pica pica* become scarce and disappear along these rivers when they reach the hot Southwest or the more humid central plains. Subtle habitat changes may occur, but it is not clear why such an opportunistic species should be limited by them.

Concerning competitors, it is obvious that *Pica pica* is replaced by the closely related *P. nuttalli* in interior California. Magpies forage opportunistically on invertebrates (especially grasshoppers), carrion, and various other items (Linsdale, 1937; Verbeek, 1973). It is very difficult to describe the foraging niche of such a species, but the Common Crow (*Corvus brachyrhynchos*) and White-necked Raven (*C. cryptoleucus*) appear generally similar in food and habitat requirements (Bent, 1946). The White-necked Raven is a bird of the Southwest. The Common Crow is distributed all across the United States, but is especially abundant in central and eastern regions (Bystrak, 1974). While these two species of *Corvus* do roughly circumscribe the range of the Black-billed Magpie, we would be reluctant to conclude, without more field evidence, that they are involved in a competitive exclusion. First, the White-necked Raven is uncommon (Bystrak, 1974) and more typical of southwestern grasslands than the actual hot desert country (Phillips et al., 1964) marking the boundary of magpie distribution. Second, the Common Crow is, in fact, widely sympatric with the Black-billed Magpie. Linsdale (1937) reports only occasional and mild interactions between crows and magpies. Verbeek (1973) observed a number of interactions between crows and *Pica nuttalli*; however, these occurred only around the nest and may have involved a response to the crows as potential nest predators. At other seasons the two species were tolerant of each other. Finally, *Pica pica* is Holarctic in distribution and in Great Britain and Europe is sympatric with four species of *Corvus* with generally similar habitat requirements (Bannerman, 1953).

We would like to conclude by returning to the question of climate. It seems very likely that the Black-billed Magpie (and/or their invertebrate prey) cannot tolerate the extreme temperatures of a warm desert. Verbeek (1972:571) noted that *Pica nuttalli* forage in summer mainly in the morning, partly because midday heat even in California stops the activity of invertebrate prey, and partly because "this same heat severly limits the birds in their feeding." In the Old World magpies are distributed throughout Europe and into North Africa as far as the edge of the Sahara (Bannerman, 1953). In New Mexico *Pica pica* breeds only in the northern third of the state; yet in the cooler winter season birds may wander down the Rio Grande Valley considerable distances (Ligon, 1961).

While the eastern distributional limits of the Black-billed Magpie do not fit with striking physiographic or habitat changes, they do coincide with major changes in climatic regime which appear to have general avifaunal significance. For example, Salt (1952) concluded that the House Finch (*Carpodacus mexicanus*) does not breed eastward in the Great Plains because of its intolerance of high summer humidity. The eastern limits of this species are very similar to those of the magpie.

The eastward disappearance of *Pica pica* also is generally coincidental with rather steep zones of introgression between eastern and western populations of several bird species. The most familiar of these is the zone of "hybridization" between the western (*cafer*) and eastern (*auratus*) subspecies of the Common Flicker (*Colaptes auratus*), analyzed by Short (1965).

Interestingly, a third subspecies, *C. a. chrysoides*, replaces *cafer* in the Southwest, although this zone is somewhat south of the limits of magpie distribution. Johnson (1969:229) reviewed the situation in flickers and made these comments:

> One of the most striking revelations that came to me upon examining Short's generalized maps of the geographic distribution of flickers in North America is the great coincidence of phenotypic change in the various forms with major climatic boundaries on the continent.

Rising (1969), in fact, studied the comparative physiologies of Northern Orioles (*Icterus galbula*) which, in the same part of the western Great Plains as the flickers, undergo marked phenotypic change. He found that the western "Bullock's Oriole" (*I. g. bullocki*) is better adapted to hot dry climate than is the eastern "Baltimore Oriole" (*I. g. galbula*).

We suggest that climatic factors related to temperature and humidity may limit the abundance and distribution of the Black-billed Magpie, either directly or by their effects upon the availability of invertebrate prey. Future research on this interesting bird could profitably include ecophysiological studies as well as more fieldwork on the relationships of this species to subtle habitat changes or the presence of competitors, especially the Common Crow.

Acknowledgments.— We are grateful to the University of Colorado Computing Center and Taximetrics Laboratory for technical assistance, and to the many students who have helped to build the Christmas count data banks. This project was supported by grant GB 36860 from the National Science Foundation.

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NECTAR COMPOSITION OF HAWKMOTH-VISITED SPECIES OF *OENOTHERA* (ONAGRACEAE)

Robert E. Stockhouse, II[1]

Abstract. Nectars of 11 hawkmoths-visited taxa of *Oenothera* were studied. Qualitatively the sugars of all taxa were identical. The amount of nectar produced per night among the taxa was quite variable. Potential energy available from nectar of an average flower of *O. caespitosa* was determined to be 42.1 calories.

There is little information on the amount of nectar produced, its composition, or nutritive potential for hawkmoth-visited flowers. (Gregory, Aliso 5:357-419), 1963/64); (Heinrich and Raven, Science 176:597-602, 1972); (Handel et al., Am. Jour. Bot. 59:1030-1032, 1972); Baker and Baker, Studies of nectar—constitution and pollinator—plant coevolution. Pages 100-140 *in* Coevolution of Animals and Plants). The nectars of 10 hawkmoth-visited taxa of *Oenothera* were studied to determine quantity and sugar composition available to nocturnal visitors.

Methods.— Nectar was collected in capillary tubes (5 microliter) in the field or from plants grown in the greenhouse. The component sugars were determined using paper chromatography. Whatman No. 1 filter paper (5" x 18") was spotted with 5 microliters of nectar from each species and three standard sugars. Each chromatogram was run in butanol, ethanol, and water (10:6:4 v/v/v) for 44 hours until the solvent had nearly reached the end of the paper. The chromatograms were allowed to dry and were sprayed with a sugar spray (80 ml of 95% ethanol, 10 ml of 40% TCA, and 10 ml of glacial acetic acid, which was saturated with benzidine dihydrochloride), which made the sugars visible. The percentage sugar was determined with a Bausch & Lomb low-range hand refractometer.

Results and Discussion.— The nectar sugar composition of eight species of *Oenothera* is presented in Table 1. Qualitatively the eight species have identical nectar sugars, consisting of glucose, fructose, sucrose, and an unknown (probably raffinose). Quantitative measurements were not made, although it appeared from the chromatograms that there were differences in the quantity of the sugars produced among taxa.

The amount of nectar produced per night was determined for four species (Table 2). *Oenothera caespitosa* produced the largest volume of nectar, averaging 35 microliters per flower (volumes were averaged for subspecies *jonesii*, *marginata*, and *montana*). Nectar was usually within 4 cm of the top of the hypanthium in *O. caespitosa* when the flowers opened. *Oenothera eximia* and *O. muelleri* averaged 20 microliters per night. Nectar of *O. eximia* was much nearer the hypanthial opening than it was in *muelleri* (Table 2). Proboscid lengths for hawkmoths visiting *O. muelleri* must be very long (at least 13 cm) if they are to gain access to the nectar. *Oenothera primiveris* produced on the average only 8 microliters of nectar per night.

Heinrich (J. Exp. Biol. 55:223-239, 1971) determined that the 3-gram hawkmoth, *Manduca sexta*, expends approximately 11 calories of energy per minute while hovering and somewhat less while flying. *Manduca quinquemaculata* and *Sphinx chersis*, both pollinators of *O. caespitosa* (unpublished data), are approximately the same size as *M. sexta* and probably have similar energy requirements for flight.

Table 1. Nectar composition of eight species of *Oenothera*.

Species	Glucose	Fructose	Sucrose	Unknown #1
albicaulis	+	+	+	+
caespitosa ssp.				
caespitosa	+	+	+	+
jonesii	+	+	+	+
marginata	+	+	+	+
purpurea	+	+	+	+
eximia	+	+	+	+
macrosceles	+	+	+	+
maysillesii	+	+	+	+
muelleri	+	+	+	+
primiveris	+	+	+	+
psammophila	+	+	+	+

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Table 2. Summary of the amount of nectar produced per night by six hawkmoth-visited species of *Oenothera*.

Species	Average % sugar	Nectar volumes: Average in microliters	Nectar volumes: Range in microliters	Average height of nectar in hypanthium (cm)	Average length of hypanthium (cm)
caespitosa	32.5	35	18-69	5.2	9.4
eximia	35.0	20	5-32	4.0	5.5
hookeri	26.0	--	--	--	--
muelleri	29.5	20	17-23	3.0	16.0
primiveris	34.0	8	4-9	3.0	5.0
xylocarpa	33.5	--	--	--	--

The amount of potential energy available from an average flower of *O. caespitosa* was calculated. The flowers averaged 35 microliters of nectar per night, of which approximately 32.5% was sugar. [Of the 35 microliters approximately 25.5 (73%) were available when the flower opened at sunset, 6 additional had been produced by 9:15 p.m., the remainder by 8 a.m. the following morning.] Assuming there are approximately 3.7 calories per mg of glucose (Heinrich and Raven, Science 176: 597-602, 1972) there are 42.1 calories per flower per night available for hawkmoths [35 mg nectar/flower x 0.325 (sugar concentration) x 3.7 calories/mg sugar = 42.1 calories per flower.] Even as a rough approximation, it is clear that each flower is a large potential energy source for hawkmoths. Even in small populations with only 20-50 flowers open on a given night, 42 calories per flower would offer a large energy reward for the hawkmoth pollinators.

Acknowledgments.— I wish to thank Steve and Susan Chaplin and Pat Wells for helpful comments on this manuscript. This study was supported in part by a grant-in-aid of research from the Scientific Research Society of North America.

A REVISION OF THE NEARCTIC SPECIES OF *CLINOHELEA* KIEFFER (DIPTERA: CERATOPOGONIDAE)

William L. Grogan, Jr.[1] and Willis W. Wirth[2]

Abstract.—The seven species of *Clinohelea* known to inhabit North America are described and illustrated, and a key is provided for identification. Two species groups are recognized: the *unimaculata* group and the *bimaculata* group. *Clinohelea longitheca* and *C. pseudonubifera* are new. *Clinohelea nebulosa* (Malloch) is a synonym of *C. curriei* (Coquillett) NEW SYNONYMY.

Clinohelea Kieffer is a fairly small genus of ceratopogonids, worldwide in distribution. Little is known of their biology; but the adult females are predaceous on other insects, and the larvae are aquatic. The five previously known North American species were described by Loew (1861), Adams (1903), Coquillett (1905), Malloch (1915), and Wirth (1952). Most of these species were originally described in the genus *Ceratopogon* Meigen and later transferred to *Palpomyia* Meigen, *Johannseniella* Williston, or *Johannsenomyia* Malloch. Although Johannsen (1943) correctly placed these species in *Clinohelea*, the North American species have needed comprehensive revision and a good key for identification.

In the present paper seven Nearctic species of *Clinohelea*, two of which are new, are described and illustrated. Two species groups are recognized and given the names of the oldest named species in their group. All of the types of *Clinohelea* species from North America have been examined, as well as examples of 17 species from other parts of the world. All specimens examined unless otherwise noted are part of the collection of the National Museum of Natural History (USNM) in Washington. In the lists of specimens examined, slide-mounted specimens are denoted (S), and pinned specimens as (P). The types of our new species will be deposited in the USNM.

Measurements and other data are based on slide-mounted specimens and are recorded in the manner of Chan and LeRoux (1965). When possible, 10 females of each species were critically measured. The data are presented in the following manner: mean value (minimum value - maximum value, n = number of measurements), except in the case of new species, where the actual values are given for the holotype, and the mean, minimum-maximum, and number of measurements are given in the variation section. Numerical characters for female Nearctic *Clinohelea* are presented in Table 1.

For general terminology of Ceratopogonidae see Wirth (1952) and Chan and LeRoux (1965). The following special terms are used in the descriptions of females. Wing length is measured from the basal arculus to the wing tip. Antennal proportions (AP) are the relative lengths of each flagellomere; antennal ratio (AR) is the length of the proximal 8 flagellomeres, divided into the length of the distal 5 flagellomeres. Palpal ratio (PR) is the length of the 3rd palpal segment divided

Table 1.—Numerical characters of female Nearctic *Clinohelea* (minimum-maximum values).

Species	Wing length (mm)	Wing breadth (mm)	Costal ratio	Palpal ratio	Antennal ratio	Femoral spines		
						Fore	Mid	Hind
UNIMACULATA GROUP								
curriei	2.53-3.23	0.81-0.94	0.81-0.87	3.20-4.50	1.50-1.66	0-3	0-2	1-3
nubifera	2.32-2.42	0.71-0.77	0.85-0.86	4.00-4.36	1.41-1.46	0	0-3	2-4
pseudonubifera	2.03-2.19	0.65-0.69	0.82-0.83	2.86-3.00	1.35-1.38	0	0-1	0-1
BIMACULATA GROUP								
bimaculata	1.65-2.68	0.50-0.74	0.82-0.86	2.60-3.40	1.17-1.36	0	0	0-3
dimidiata	2.32-2.74	0.68-0.87	0.76-0.82	3.17-3.80	1.25-1.40	0	0	0
usingeri	2.50-2.74	0.70-0.81	0.80-0.81	3.17-3.67	1.29-1.35	0	0	0
longitheca	1.97-2.00	0.61	0.82-0.84	2.89-3.11	1.17-1.36	0	0	0

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by its greatest breadth. Terminology dealing with male genitalia follows that of Snodgrass (1957) and Chan and LeRoux (1965). All female genitalia and spermathecae have been drawn to the same scale. Types have been illustrated whenever possible.

We are especially indebted to Mrs. Ethel L. Grogan for preparation of the illustrations. Thanks are also extended to the following persons and their institutions for the loan of type and other material or information regarding specimens in their collections: Donald W. Webb, Illinois Natural History Survey, Urbana (INHS); George W. Byers, Snow Entomological Museum, University of Kansas, Lawrence (KU); Wilford J. Hanson, Utah State University, Logan (USU); and Janice C. Scott, Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ).

Genus *Clinohelea* Kieffer

Clinohelea Kieffer, 1917: 295. Type-species, *Ceratopogon variegatus* Winnertz, by original designation.

Diagnosis.— Moderately large, shining ceratopogonids, usually with infuscated wings; body nearly bare, rather slender; pleuron usually with transverse silvery band. Eyes bare; widely separated. Antenna slender; flagellomeres 1-8 long, flagellomeres 9-13 elongate in female; flagellomeres 11-13 elongate in male; plume sparse in male. Palpus slender; 3rd segment slender, lacking a pit. Female mandible with coarse teeth. Mesonotum moderately robust, without humeral pits, a short anterior tubercle sometimes present. Femora slender, occasionally with up to four spines; 4th tarsomere of at least mid and hind legs deeply bilobed, each lobe ending in a stout blunt spine and smaller spines; fore 5th tarsomere greatly swollen in both sexes; fore claws equal, mid and hind very unequal in female; all claws equal in male. Wing long, without macrotrichia; costa extending to 0.75 but not more than 0.90 of wing length; two radial cells present, 2nd much longer than 1st; no intercalary fork; medial fork broadly sessile. Female abdomen without eversible glands or gland rods; genital sclerotization small, simple; two well-developed spermathecae. Male genitalia with 9th sternum short, broad; 9th tergum tapered with large cerci; basimere and telomere relatively long and slender; aedeagus with low anterior arch, distal portion broad, underlying membrane extending beyond tip; claspettes usually divided, each portion slender withan elongated bulbous tip.

Immature stages.— Larvae are aquatic. Wirth (1951) described the pupa of *C. bimaculata*, which he reared from the sandy margin of a small stream in Virginia. This is apparently the only Nearctic species that has been described in an immature stage.

Adult habits.— Adults can be found on vegetation bordering water, and Grogan has taken them at flowers and from a small grove of trees in Utah. Downes (1960, 1971) stated that adult females are predaceous on other small insects that are captured in flight, but did not give specific examples.

Key to the Nearctic Species of *Clinohelea* (primarily Females)

1. Fore 5th tarsomere solid brown; wing with two spots, one centered over 1st radial cell, second near tip of costa (*bimaculata* group) 2
Fore 5th tarsomere with pale band; wing with 1 spot centered over 1st radial cell or entirely infuscated (*unimaculata* group) 5

2. Spermathecae large, elongated, ellipsoid .... *longitheca* n. sp.
Spermathecae small, spheroid to ovoid 3

3. Legs predominantly yellow, distal one-fourth of hind femur brown .... *bimaculata* (Loew)
Legs predominantly brownish, distal one-half of hind femur brown 4

4. Tibiae entirely brown; basal arms of male aedeagus separated .... *dimidiata* (Adams)
Tibiae yellowish in midportion, basal and apical portions brown; basal arms of male aedeagus intact .... *usingeri* Wirth

5. Wing with narrow dark infuscation extending from apex of costa to tip .... *nubifera* (Coquillett)
   Wing without narrow dark infuscation at tip 6

6. Fore 5th tarsomere with pale band twice as long as width of tarsomere .... *curriei* (Coquillett)
   Fore 5th tarsomere with pale band much shorter than width of tarsomere .... *pseudonubifera* n. sp.

UNIMACULATA GROUP

Wing with infuscation usually centered over 1st radial cell or entirely infuscated. Fore 5th tarsomere with pale band. At least hind femur with spines usually present. Species examined in this group not from North America: *C. unimaculata* (Macquart), Europe.

Clinohelea curriei (Coquillett)

(Fig. 1, 6a)

Ceratopogon curriei Coquillett, 1905: 62 (female; British Columbia)

Palpomyia curriei (Coquillett); Malloch 1914: 219 (combination; description; key)

Clinohelea curriei (Coquillett); Johannsen, 1943: 783 (combination); Wirth, 1965: 136 (distribution)

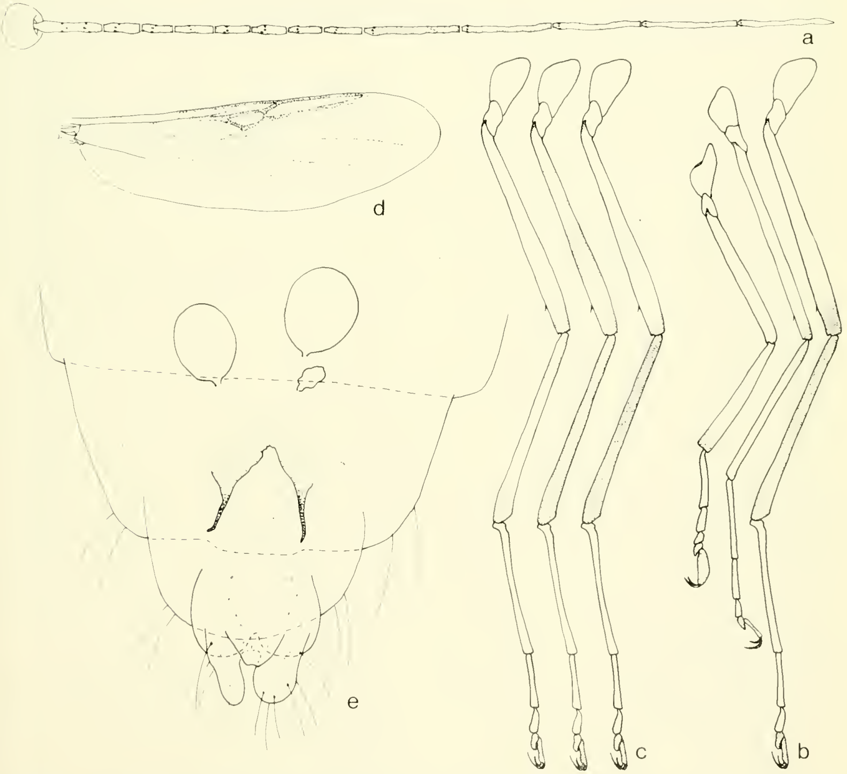

Fig. 1. *Clinohelea curriei* (Coquillett) female: a, antenna; b, leg pattern; c, variations in hind leg pattern; d, wing; e, genitalia.

Palpomyia nebulosa Malloch, 1915: 322 (female; Michigan). NEW SYNONYMY

Clinohelea nebulosa (Malloch); Johannsen, 1943: 783 (combination); Wirth, 1965: 136 (distribution)

Diagnosis.— Distinguished from all other Nearctic *Clinohelea* by the following combination of characters: fore 5th tarsomere with pale band longer than width of 5th tarsomere; wing with infuscation centered over 1st radial cell or entirely infuscated.

Female.— Wing length 2.78 (2.53-3.32, n = 10) mm; breadth 0.85 (0.81-0.94, n = 10) mm.

Head: Brown. Antenna (Fig. 1a) slender; pedicel yellow to pale brown; basal flagellomere with proximal two-thirds pale, distal one-third brown; remaining flagellomeres brown; AP 22-10-10-10-10-10-11-12-30-28-29-29-31 (n = 10); AR 1.57 (1.50-1.66, n = 10). Palpus brown; 3rd segment longer than 5th; PR 4.03 (3.20-4.50, n = 10). Mandible like that of *C. bimaculata* (Fig. 4c).

Thorax: Mesonotum, scutellum, postscutellum dark brown. Legs (Fig. 1b) yellow; apex of fore tibia, mid femorotibial area, fore distal 3 tarsomeres, mid and hind 4th and 5th tarsomeres brown; hind leg pattern variable, most common form (Fig 1b) with distal one-sixth of femur and tibia brown, other hind leg patterns as in Figure 1c; fore 5th tarsomere with pale band longer than width of tarsomere; 0-3 fore, 0-2 mid, and 1-3 hind femoral spines. Wing (Fig. 1d) usually with infuscated area centered over 1st radial cell or entirely infuscated; veins brown; CR 0.84 (0.81-0.87, n = 10). Halter pale.

Abdomen: Brown. Genitalia as in Figure 1e with a pair of slender, posteriorly directed sclerotized arms arising anteriorly from a lighter sclerotized area. Spermathecae small, spheroid to ovoid, subequal to unequal with short necks.

Male.— Similar to female with following differences: smaller; antennal pedicel dark brown, flagellum brown; legs more diffused with brown; 0-1 fore, 0-1 mid, and 0-2 hind femoral spines. Genitalia form and shape like that of *C. bimaculata* (Fig. 4f); aedeagus as in Figure 6a.

Distribution.— Alaska and California to Newfoundland and Florida (locality records plotted in Figure 3).

Types.— Holotype female of *C. curriei*, Kaslo, British Columbia, 17 June 1903, R. P. Currie (Type no. 8361, USNM); holotype female of *C. nebulosa*, Grand Junction, Van Buren Co., Michigan, 15 July 1914, C. A. Hart (INHS).

Specimens examined.— 82 slides, 218 pinned specimens from:

ALASKA: Anchorage (Aldrich); Matanuska (Chamberlin). CALIFORNIA: Eldorado Co., Luther Pass (Schlinger, Univ. Calif. Davis). CONNECTICUT: Fairfield Co., Redding (Melander); Tolland Co., Storrs (Melander). DELAWARE: New Castle Co., Delaware City. FLORIDA: Alachua Co., Gainesville (Wirth). IDAHO: Ada Co., Boise (INHS); Nez Perce Co., Sweetwater (Aldrich). INDIANA: Porter Co., Mineral Springs (INHS). IOWA: Hancock Co., Pilot Knob St. Park (Gaud). MAINE: Hancock Co., Bar Harbor (Johnson). MASSACHUSETTS: Franklin Co., Rowe (Coher); Middlesex Co., Bedford (Wirth); Concord (Wirth); Suffolk Co., Boston (Melander). MICHIGAN: Cheboygan Co. (Dreisbach), Douglas Lake (Williams); Clare Co. (Dreisbach); Iron Co. (Dreisbach); Lake Co. (Dreisbach); Livingston Co., George Reserve (Sabrosky, Steyskal); Manistee Co. (Dreisbach); Midland Co. (Dreisbach); Nottawa (Sabrosky, Dreisbach); Missaukee Co. (Dreisbach); Osceola Co. (Dreisbach); Roscommon Co. (Dreisbach); Van Buren Co., Grand Junction (Hart, holotype of *nebulosa*); Wexford Co., (Dreisbach). MINNESOTA: Ramsey Co. (Wall). NEBRASKA: Cherry Co., Hackberry Lake (Wirth), Pelican Lake (Wirth). NEW HAMPSHIRE: Grafton Co., Stinson Lake (Wirth). NEW YORK: Chautauqua Co., S. Dayton (Wirth); Erie Co., East Aurora (Van Duzee), East Concord Bog (Wirth); Franklin Co., Adirondacks (Melander); Lewis Co., Brantingham Lake (Wirth), Letchworth St. Park (Wirth), Whetstone Gulf (Wirth); Monroe Co., Braddock Bay (Wirth); Orleans Co., Albion (Wirth); St. Lawrence Co., Cranberry Lake (Wirth); Suffolk Co., Cold Spring Harbor (Melander); Tompkins Co., Ringwood Reserve (Wirth). OHIO: Summit Co. (Lipovsky, KU). UTAH: Cache Co., Hyrum (Grogan). VERMONT: Caledonia Co., Lyndon (Melander). VIRGINIA: Alexandria (Wirth); Fairfax Co., Dead Run (Wirth). WISCONSIN: Polk Co. (Baker, paratype of *nebulosa*, INHS). WEST VIRGINIA: Pocahontas Co., Cranberry Glades (Wirth, Sabrosky). BRITISH COLUMBIA: Kaslo (Currie, holotype of *curriei*). Quebec: Meach Lake (Wirth). NEWFOUNDLAND: Squire's Mem. Park (Alexander). NOVA SCOTIA: Baddeck (Fairchild). ONTARIO: Algonquin Park (Wirth); Kemptville (Wirth); Ottawa (Melander, Wirth); Toronto (Van Duzee); Waubamick (Melander).

Discussion.— The Palaearctic species, *C. unimaculata* (Macquart) closely resembles *C. curriei*. However, the hind tibia is pale except for the narrow base and apex; the apices of the fore and mid femora are conspicuously dark, narrowly on the fore leg but more broadly on the mid leg; and the hind femur lacks any trace of infuscation except the conspicuous apical dark band.

Clinohelea nubifera (Coquillett)

(Fig. 2a, c, e, g; 6b)

Ceratopogon nubifer Coquillett, 1905: 61 (female; Florida)

Palpomyia nubifera (Coquillett); Malloch, 1914: 217 (combination; key)

Clinohelea nubifera (Coquillett); Johannsen, 1943: 783 (combination); Wirth, 1965: 136 (distribution)

DIAGNOSIS.— Distinguished from all other Nearctic *Clinohelea* by the following combination of characters: wing with infuscation centered over 1st radial cell and a narrow infuscated band extending from apex of costa to wing tip; and fore 5th tarsomere with pale band.

FEMALE.— Wing length 2.35 (2.32-2.42, n = 3) mm; breadth 0.74 (0.71-0.77, n = 3) mm.

Head: Vertex and proboscis brown, frontoclypeus lighter brown to yellowish. Antenna (Fig. 2a) slender; pedicel yellow to light brown; proximal 5-8 flagellomeres pale on basal portions, distal portions light brown; distal 5 flagellomeres brown; AP 26-12-11-11-11-11-11-12-32-29-30-30-30 (n = 3); AR 1.43 (1.41-1.46, n = 3). Palpus

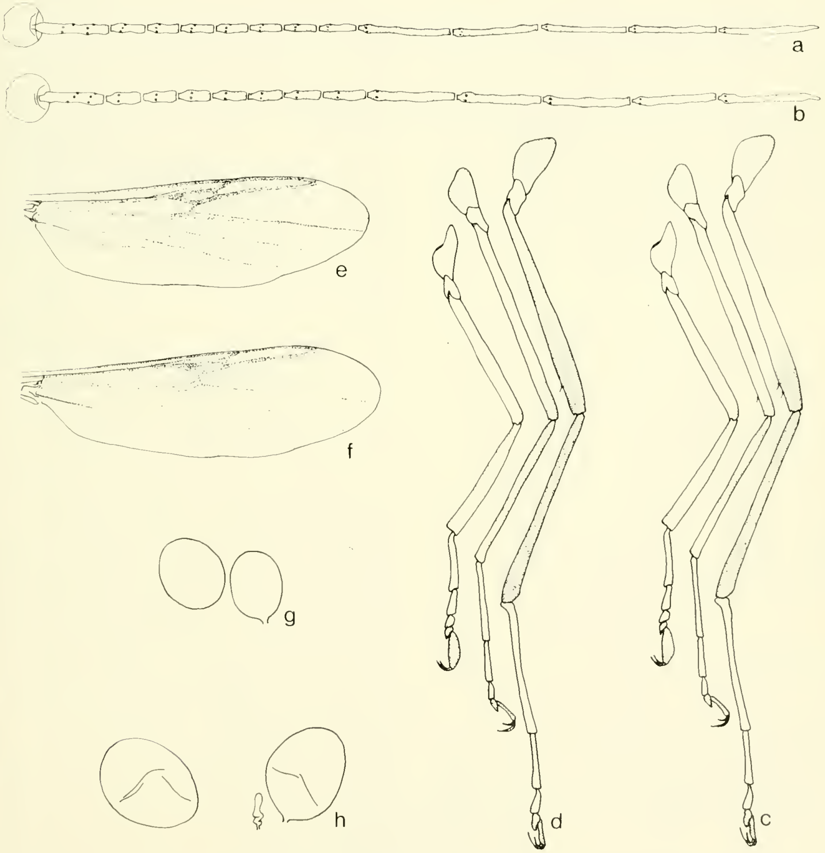

Fig. 2. Female *Clinohelea*: a,c,e,g, *C. nubifera* (Coquillett); b,d,f,h, *C. pseudonubifera* n. sp.; a,b, antennae; c,d, leg patterns; e,f, wings; g,h, spermathecae.

brown; 3rd segment nearly twice as long as 5th; PR 4.12 (4.00-4.36, n = 3). Mandible like that of *C. bimaculata* (Fig. 4c).

Thorax: Mesonotum, scutellum, postscutellum dark brown. Legs (Fig. 2c) yellow; proximal portions of mid and hind coxae, distal portion of hind femur, apices of fore and mid femora, all of hind tibia, proximal one-half of fore and mid tibiae, and 4th and 5th tarsomeres brown; fore 5th tarsomere with pale band shorter than width of tarsomere; 0-2 mid and 2-4 hind femoral spines. Wing (Fig. 2e) veins brown; infuscated area centered over 1st radial cell, and narrow infuscated band extending from apex of costa to tip; CR 0.86 (0.85-0.86, n = 3). Halter stem brownish; knob pale.

Abdomen: Brown. Spermathecae (Fig. 2g) small, ovoid, subequal with short necks.

MALE.— Unknown. A female specimen from Santa Rosa Co., Florida, had male genitalia mounted with her on a slide. These male genitalia were remounted in an attempt to examine them in detail. The overall shape and form of the genitalia are like that of *C. bimaculata* (Fig. 4f); aedeagus as in Figure 6b.

DISTRIBUTION.— Florida, New York (locality records plotted in Figure 3).

TYPE.—Holotype, female, Jacksonville, Florida, Mrs. A. T. Slosson (Type no. 8357, USNM, pinned).

SPECIMENS EXAMINED.— From the following localities:

FLORIDA: Alachua Co., Gainesville (Blanton), 2 females (S); Jacksonville (Slosson, holotype female, P); Highland Co., Sebring (Wirth), 1 female (P); Santa Rosa Co., Blackwater River (Fairchild), 1 female (S). NEW YORK: Suffolk Co., Cold Spring Harbor (Melander), 1 female (P).

Clinohelea pseudonubifera Grogan and Wirth, n. sp.

(Fig. 2b, d, f, h; 6c)

Clinohelea species 1; Wirth, 1951: 321 (females; Virginia).

DIAGNOSIS.— Most closely related to *C. nubifera*, and can be distinguished from all other Nearctic *Clinohelea* by the following combination of characters: fore 5th tarsomere with very short, pale band, legs mostly yellow with hind tibia and distal five-sixths of hind femur brown, and wing

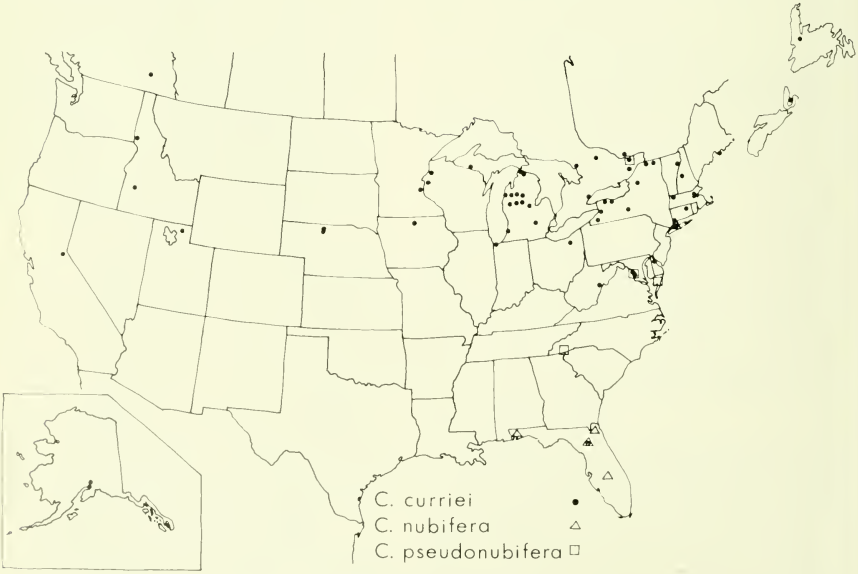

Fig. 3. North American locality records for *Clinohelea* of the *unimaculata* group.

with infuscation centered over 1st radial cell.

Female holotype.— Wing length 2.03 mm; breadth 0.65 mm.

Head: Vertex and proboscis brown; frontoclypeus lighter brown. Antenna (Fig. 2b) slender; pedicel yellow, proximal 4 flagellomeres pale, distal 9 flagellomeres brown; AP 17-9-9-8-9-9-9-10-21-21-21-21-26; AR 1.38. Palpus brown; 3rd segment about as long as 5th; PR 3.00. Mandible like that of *C. bimaculata* (Fig. 4c).

Thorax: Mesonotum, scutellum, postscutellum dark brown. Legs (Fig. 2d) yellow; proximal portions of coxae, distal five-sixths of hind femur, distal one-fifth of mid femur, mid and hind tibiae, and 4th and 5th tarsomeres of tarsi brown; fore tibia very light brown; fore 5th tarsomere with very short, pale band; mid and hind femora with 1 spine. Wing (Fig. 2f) with dark infuscation centered over 1st radial cell; veins brown; CR 0.83. Halter pale with dark brown spot on knob.

Abdomen: Brown. Spermathecae (Fig. 2h) small, ovoid, subequal, with short necks.

Male allotype.— Similar to female holotype with the following differences: smaller; antennal pedicel dark brown, flagellum brown; femora lacking spines. Genitalia shape and form like that of *C. bimaculata* (Fig. 4f); aedeagus as in Figure 6c.

Etymology.— The name *pseudonubifera* refers to the resemblance to *C. nubifera*.

Variation.— The following characters were recorded for the single female topotype: wing length 2.19 mm; breadth 0.69 mm. AR 7.35. PR 2.86. CR 0.82 The general coloration of all of the paratypes is like that of the holotype. Femoral spines ranged from 0-1 mid, and 0-1 hind.

Distribution. —Ontario to North Carolina (locality records plotted in Figure 3).

Types.— Female holotype, male allotype, 1 female paratype, Snow Hill, Worcester Co., Maryland, 2 June 1968, W. H. Anderson, light trap (Type no. 66495, USNM). Other paratypes, 4 pinned females as follows: NORTH CAROLINA: Macon Co., Highlands, 15 June 1957, J. R. Vockeroth, 1 female (Canada Nat. Coll.). ONTARIO: Ottawa, Mer Bleue, 23 June 1952 G. E. Shewell, 1 female (CNC). VIRGINIA: Fairfax Co., Falls Church, 4 July 1950, W. W. Wirth, 2 females.

Discussion.— Wirth (1951) in reference to the two female specimens from Falls Church, Virginia, stated that they were close to *C. nubifera* and *C. dimidiata* but declined to name them at the time.

Bimaculata Group

Wing with two infuscated areas, one centered over 1st radial cell, the other near tip of costa. Fore 5th tarsomere uniformly brown. Femora usually lacking spines, or if present, only on hind femur. Species examined in this group not from North America: *C. barrettoi* Lane and Duret, Brazil; *horacioi* Lane, Brazil; *neivai* Lane, Brazil; *nigripes* Macfie, Brazil; *pachydactyla* Kieffer, Singapore; *rubriceps* Kieffer, Paraguay; *saltanensis* Lane and Duret, Argentina; *townesi* Lane, Brazil; *townsendi* Lane, Brazil.

Clinohelea bimaculata (Loew)

(Fig. 4, 6d)

Ceratopogon bimaculatus Loew, 1861: 311 (female; Washington, D.C.).

Johannseniella bimaculata (Loew); Malloch, 1914: 226 (combination; description; key).

Johannsenomyia bimaculata (Loew); Malloch, 1915: 332 (combination; key).

Clinohelea bimaculata (Loew); Kieffer, 1917: 317 (combination; key; fig. tarsus); Wirth, 1951: 321 (description and fig. pupa); Johannsen, 1952: 164 (key, fig. tarsus); Wirth, 1965: 136 (distribution).

Diagnosis.— Distinguished from all other Nearctic *Clinohelea* by the following combination of characters: legs mainly yellow with a dark subapical band on the hind femur, two-spotted wings, and antennal pedicel yellow.

Female.— Wing length 2.06 (1.65-2.68, n = 10) mm; breadth 0.63 (0.50-0.74, n = 10) mm.

Head: Frontovertex brown; proboscis and palpus pale yellow. Antenna (Fig. 4a) slender; pedicel yellow, proximal 8 flagellomeres brown, distal 5 flagellomeres lighter brown; AP 20-11-10-10-10-10-11-12-24-23-23-23-25 (n = 10); AR 1.24 (1.17-1.36, n = 10). Palpus with 3rd segment slightly longer than 5th; PR 2.87 (2.60-3.40, n = 10). Mandible (Fig. 4c)

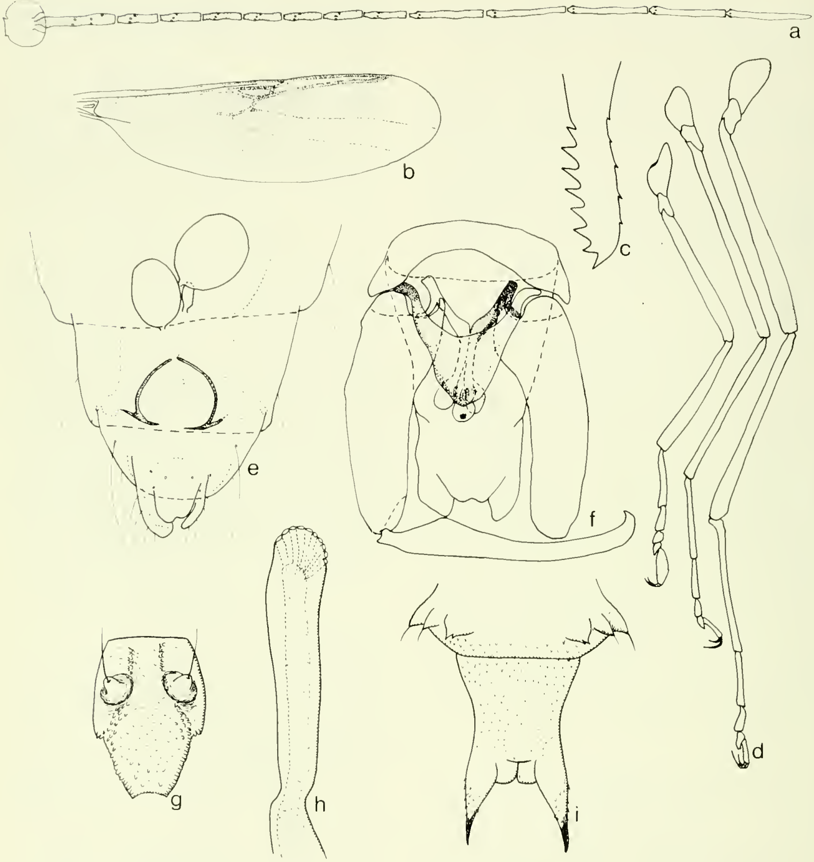

Fig. 4. *Clinohelea bimaculata* (Loew): a-e, female; f, male genitalia; g-i, pupa; a, antenna; b, wing; c, mandible; d, leg pattern; e, genitalia; g, operculum; h, respiratory organ; i, anal segment.

heavily sclerotized; inner margin with six to nine large coarse teeth; outer margin with four or five small teeth.

Thorax: Mesonotum, scutellum, postscutellum brown. Legs (Fig. 4d) yellow; proximal portion of hind coxa, subapical band on hind femur, and 4th and 5th tarsomeres brown; hind femur with 0-3 spines. Wing (Fig. 4b) veins brown; infuscations centered over 1st radial cell and just before tip of costa; occasionally, infuscated areas joined posteriorly; CR 0.84 (0.82-0.86, n = 10). Halter stem pale yellowish; knob white.

Abdomen: Brown to reddish brown. Genitalia as in Figure 4e with a pair of slender, sclerotized, anteriorly directed arms arising from shorter, thicker arms. Spermathecae small, spheroid to ovoid, subequal to unequal, with short necks.

Male.— Similar to female with the following differences: smaller; antennal pedicel brown; hind femur lacking spines. Genitalia as in Figure 4f. Ninth sternum about three times broader than long, base slightly curved with a caudomedial excavation; 9th tergum tapered distally to a rounded tip, cerci short, not reaching apex of basimeres. Basimere slightly curved, 2.5 times longer than broad; telomere slightly longer than basimere, curved, tapered distally with pointed, hooked tip. Aedeagus (Fig. 6d) heavily sclerotized, triangular, about as broad as long; basal arm recurved about 90 degrees, heavily sclerotized; distal portion with blunt pointed tip; underlying membrane extending beyond tip, rounded with a dark spot. Claspettes divided; basal arm heavily sclerotized, recurved; distal portion more lightly sclerotized, tip elongate, bulbous.

Pupa.— Length 3.5 mm; color light brown. Operculum (Fig. 4g) narrow; 0.9 times as broad as long with a pair of rounded tubercles bearing long seta; surface with fine tubercles, those on lateral margin sharp and setose. Respiratory horn (Fig. 4h) moderately long and slender, about five times longer than broad with 10 apical spiracular papillae. Anal segment (Fig. 4i) about twice as long as broad; surface covered with fine tubercles; apicolateral processes about one-third of total length, with subapical fine tubercles; tips heavily sclerotized and sharply pointed.

Distribution.— Michigan and Texas to New Hampshire and Florida (locality records plotted in Figure 7).

Type.— Holotype, female, Washington, D.C., Osten-Sacken coll. (Type no. 10379, MCZ).

Specimens examined.— 177 slides, 158 pinned specimens from:

ALABAMA: Mobile Co., Mobile (Blanton, Cannon). CONNECTICUT: Litchfield Co., Lake Waramaug (Melander). DISTRICT OF COLUMBIA: Washington (Coquillett). FLORIDA: Alachua Co., Gainesville (Blanton, Wirth); Baker Co., Olustee (Blanton); Bay Co., Panama City Beach (McElvey); Calhoun Co., Blountstown (Blanton); Collier Co., Collier Seminole St. Park (Wirth), Ochopee (Blanton); Escambia Co., Bratt (Blanton); Glades Co., Palmdale (Irons); Gulf Co., 2 mi. N Beacon Hill (Blanton), Wewahitchka (Blanton); Hardee Co., Ona (Irons); Highlands Co., Archbold Biol. Sta. (Wirth), Lake Placid (Layne), Sebring (Wirth); Indian River Co., Fellsmere (Wirth), Vero Beach (Wirth); Duval Co., Jacksonville (Knight); Jefferson Co., Monticello (Whitcomb); Lake Co., Leesburg (Braddock); Leon Co., 3 mi. N Tallahassee (Blanton); Liberty Co., Torreya St. Park (Blanton, Fairchild, Weems, Wirth); Marion Co., Juniper Springs (Wirth); Orange Co., Lake Magnolia Park (Irons), Rock Springs (Wirth); Palm Beach Co., W. Palm Beach (Hardy, KU); Putnam Co., Lon's Lake (Blanton); Sarasota Co., Myakka River St. Park (Wirth); Suwanee Co., Suwanee Springs (Beamer, KU); Wakulla Co., Ocklockonee River St. Park (Wirth); Walton Co. (Butler). GEORGIA: Charlton Co., Okefenokee Swamp (Beamer, KU); Mitchell Co., Newton (Pratt); Thomas Co., Thomasville (Palmer). ILLINOIS: Henry Co., Algonquin (INHS); Champaign Co., Urbana (Malloch, INHS); Platt Co., Monticello (Malloch, INHS); Pulaski Co., Pulaski (Malloch, INHS). INDIANA: Tippecanoe Co., Lafayette (Aldrich, Melander). LOUISIANA: East Baton Rouge Parish, Baton Rouge (Wirth). MARYLAND: Anne Arundel Co., Mayo (Wirth); Calvert Co., Chesapeake Beach (Shannon, Knab); Charles Co., Nomomonee (Wirth); Frederick Co., Thurmont (Steyskal); Montgomery Co., Glen Echo (Malloch); Prince Georges Co., Beltsville (Malloch); Worcester Co., Snow Hill (Wirth). MASSACHUSETTS: Middlesex Co., Bedford (Wirth), Concord (Wirth). MICHIGAN: Lapeer Co., Deerfield (Steyskal); Livingston Co., George Reserve (Steyskal); Midland Co., (Dreisbach); Wayne Co., Detroit (Steyskal). NEBRASKA: Nemaha Co., Peru (Harmston). NEW HAMPSHIRE: Grafton Co., Stinson Lake (Wirth). NEW YORK: Franklin Co., Adirondacks (Melander). NORTH CAROLINA: Durham Co., Nelson (Beamer, KU); Onslow Co., Jacksonville (Bohart, USU). SOUTH CAROLINA: Georgetown Co., Hobcaw House (Henry). TENNESSEE: Lake Co., Reelfoot Lake (Snow). TEXAS: Collin Co., Plano (Tucker); Kerr Co., Hunt (Wirth), Kerrville (Bottimer). VIRGINIA: Alexandria (Wirth); Fairfax Co., Falls Church, Montgomery Co., Blacksburg (Messersmith). WEST VIRGINIA: Pocahontas Co., Cranberry Glades (Wirth, Sabrosky); Taylor Co., Grafton (Steyskal).

Clinohelea dimidiata (Adams)

(Fig. 5a, e, g; 6e)

Ceratopogon dimidiatus Adams, 1903: 27 (female; Arizona).

Johannseniella dimidiata (Adams); Malloch: 226 (combination; key).

Johannsenomyia dimidiata (Adams); Malloch, 1915: 332 (combination; key).

Clinohelea dimidiata (Adams); Johannsen, 1943: 783 (combination); Wirth, 1965: 136 (distribution).

Diagnosis.— Distinguished from all other Nearctic *Clinohelea* by the two-spotted wings and dark brown tibiae; males with basal arms of aedeagus separated.

Female.—Wing length 2.54 (2.32-2.74, n = 5) mm; breadth 0.76 (0.68-0.87, n = 4) mm.

Head: Brown. Antenna (Fig. 5a) slender; brown, proximal two-thirds of basal flagellomere pale; AP 17-10-9-9-9-10-10-11-22-21-23-23-25 (n = 4); AR 1.35 (1.25-1.40, n = 4). Palpus with 3rd segment slightly longer than 5th; PR 3.43 (3.17-3.80, n = 3). Mandible like that of *C. bimaculata* (Fig. 4c).

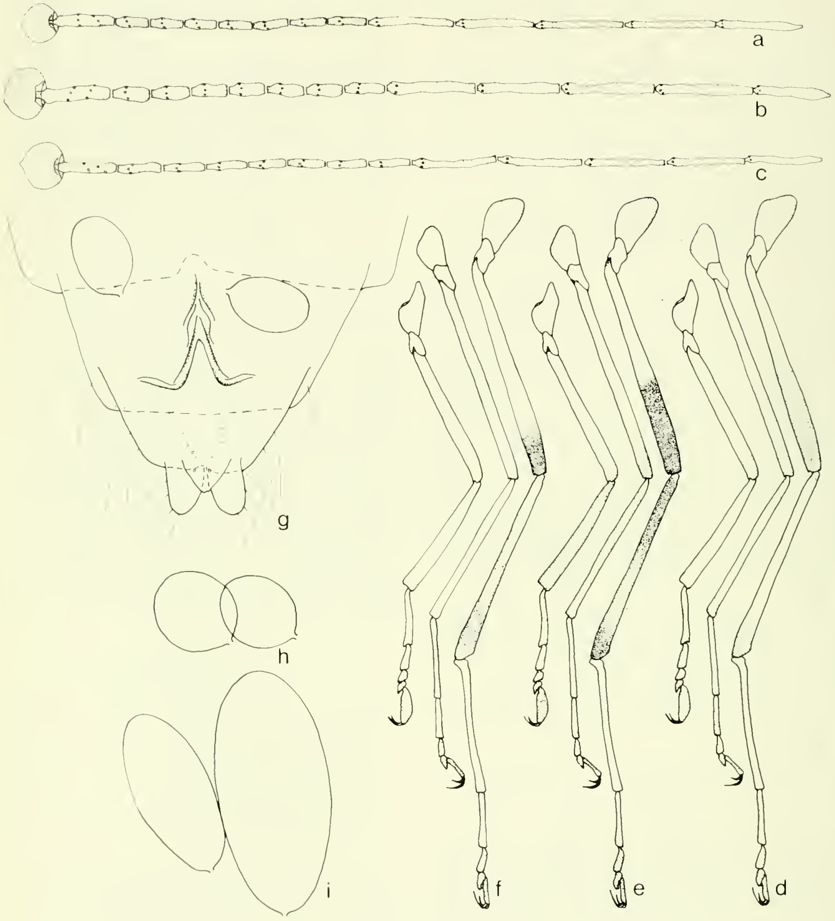

Fig. 5. Female *Clinohelea*: a,e,g, *C. dimidiata* (Adams); b,d,h, *C. usingeri* Wirth; c,f,i, *C. longitheca* n. sp.; a-c, antennae; d-f, leg patterns; g, genitalia; h, i, spermathecae.

Thorax: Mesonotum, scutellum, postscutellum dark brown. Legs (Fig. 5e) brown; yellow on fore coxa, distal one-fourth of mid and hind coxae, trochanters, most of fore femur, proximal five-sixths of mid femur, proximal half of hind femur, and mid and hind 1st and 2nd tarsomeres. Wing like that of *C. bimaculata* (Fig. 4b). Halter stem pale; knob white.

Abdomen: Brown. Genitalia as in Figure 5g with three small pairs of anteriorly directed, lightly sclerotized arms. Spermathecae small, ovoid, subequal with short necks.

Male.—Similar to the female with the following differences: smaller; flagellum entirely brown; legs more diffused with brown. Genitalia shape and form like that of *C. bimaculata* (Fig. 4f); aedeagus as in Figure 6e with basal arms apparently separated, and an anteriorly directed point on the anterior membrane.

Distribution.— Arizona, New Mexico, Utah (locality records plotted in Figure 7).

Types.— Female lectotype, 3 female paralectotypes, Grand Canyon, Coconino Co., Arizona, C. F. Adams, (KU), here designated.

Specimens examined.— From the following localities:

ARIZONA: Apache Co., Springerville (Wirth), 1 male (P); Coconino Co., Grand Canyon (Adams, types), 4 females (KU) (P). NEW MEXICO: Taos Co., Rio Grande (Wirth), 3 females (P). UTAH: Cache Co., Hyrum (Grogan), 3 females (S); Box Elder Co., Brigham City (Hardy, Stains, USU), 1 male, 1 female (S), 1 female (P); Weber Co., Huntsville (Hardy, USU), 1 female (P); Wasatch Co., Heber City (Dreisbach), 1 female (P).

Discussion.— The syntype series was labeled "G. Zuni R., Ariz., 7-27," which Adams published as "Grand Canon, Arizona" for the type locality.

Clinohelea usingeri Wirth

(Fig. 2b, d, h; 6f)

Clinohelea usingeri Wirth, 1952: 209 (female; California); Wirth, 1965: 136 (distribution).

Diagnosis.— Distinguished from all other Nearctic *Clinohelea* by the two-spotted wing and the legs mainly yellow with distal half of hind femur and apices of tibiae brown; males with basal arms of aedeagus intact.

Female.— Wing length 2.65 (2.50-2.74, n = 4) mm; breadth 0.76 (0.70-0.81, n = 3) mm.

Head: Brown. Antenna (Fig. 2b) moderately slender; basal one-half of proximal flagellomere lighter brown than remainder of flagellum; AP 17-10-9-9-9-9-9-10-23-22-22-22-20 n = 3); AR 1.33 (1.29-1.35, n = 3). Palpus with 3rd segment longer than 5th; PR 3.33 (3.17-3.67, n = 3). Mandible like that of *C. bimaculata* (Fig. 4c).

Thorax: Mesonotum, scutellum, postscutellum dark brown. Legs (Fig. 2d) yellow; proximal one-third of fore coxa, most of mid and hind coxae, distal one-half of hind femur, femorotibial areas of mid and hind fore legs, apices of tibiae, and distal 4 tarsomeres brown. Wing like that of *C. bimaculata* (Fig. 4d). Halter pale to whitish.

Abdomen: Brown. Spermathecae (Fig. 2h) small, spheroid, subequal with short necks.

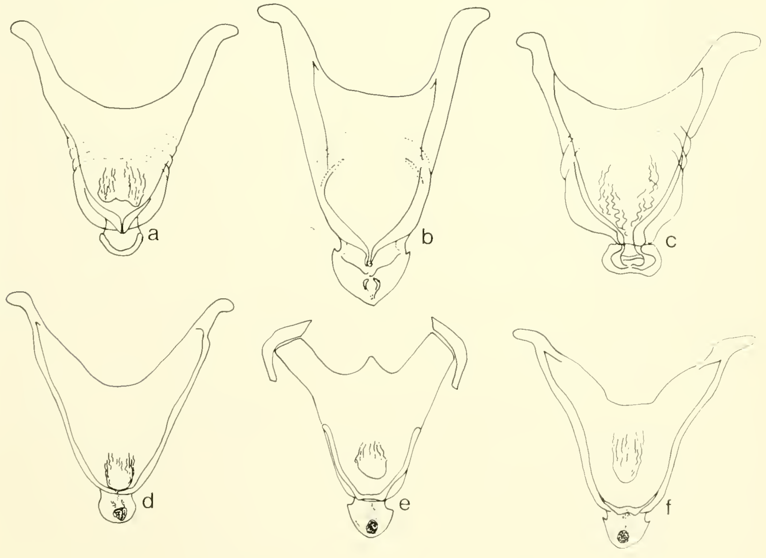

Fig. 6. Aedeagi of male *Clinohelea*: a, *C. curriei*; b, *C. nubifera*; c, *C. pseudonubifera*; d, *C. bimaculata*; e, *C. dimidiata*; f, *C. usingeri*.

MALE.— Similar to female with the following differences: smaller; flagellum entirely brown; femora and tibiae entirely brown. Genitalia shape and form like that of *C. bimaculata* (Fig. 4f); aedeagus as in Figure 6f.

DISTRIBUTION.— Arizona, California (locality records plotted in Figure 7).

TYPE.— Holotype, female, Black Lake Canyon, San Luis Obispo Co., California, 22 August 1943, W. W. Wirth (Type no. 59949, USNM).

SPECIMENS EXAMINED.— From the following localities:

ARIZONA: Cochise Co., Sunnyside Canyon (Hardy, KU), 1 male, 3 females. CALIFORNIA: San Diego Co., Live Oak Park (Melander) 1 female (P); San Luis Obispo Co., Black Lake Canyon (Wirth, type series), 1 male, 2 females (P), 3 females (S).

DISCUSSION.— Present records indicate that *C. dimidiata* is an inhabitant of the Great Basin and the Upper Colorado Plateau, while *C. usingeri* is an inhabitant of the Mojave and Sonoran deserts. Further collecting is necessary to determine whether the geographic ranges of these two closely related species overlap, or if they are separated by altitude.

Clinohelea longitheca Grogan and Wirth n. sp.

(Fig. 5c, f, i)

DIAGNOSIS.— Distinguished from all other Nearctic *Clinohelea* by the very large, unequal, elongate, ellipsoid spermathecae, the legs mainly yellow with hind tibia and distal fourth of hind femur brown, and the two-spotted wings.

FEMALE HOLOTYPE.— Wing length 2.00 mm; breadth 0.61 mm.

Head: Brown; frontoclypeus lighter brown. Antenna (Fig. 5c) slender, brown; AP 17-11-10-10-10-10-10-11-21-21-21-20-20; AR 1.17. Palpus brown; 3rd segment longer than 5th; PR 3.11. Mandible like that of *C. bimaculata* (Fig. 4c).

Thorax: Mesonotum, scutellum, postscutellum dark brownish black. Legs (Fig. 5f) yellow; most of mid and hind coxae, distal one-fourth of hind femur, hind tibia, and distal 3 tarsomeres brown; distal one-fourth of fore tibia light brown. Wing like that of *C. bimaculata* (Fig. 4d) with an infuscation over 1st radial cell and just before tip of costa. Halter light brown.

Abdomen: Brown. Spermathecae (Fig. 5i) very large, unequal, elongate ellipsoid.

MALE.— Unknown.

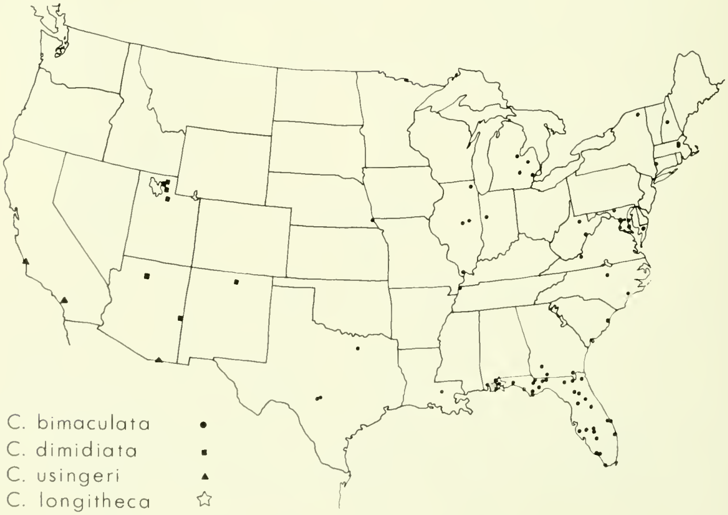

Fig. 7. North American locality records for *Clinohelea* of the *bimaculata* group.

Etymology.— The name longitheca is derived from the Latin *longus* (long) and *theca* (sac) and refers to the very large, elongate, ellipsoid spermathecae that are characteristic of this species.

Variation.— The following characters were recorded for the single female topotype: wing length 1.97 mm; breadth 0.61 mm. AR 1.36. PR 2.89. CR 0.84. The general coloration is like that of the holotype.

Distribution.— Florida (type locality plotted in Figure 7).

Types.— Female holotype, 1 female paratype (S), A. & M. Biological Station, Blackwater River State Forest, Santa Rosa Co., Florida, 21 May 1971, G. B. Fairchild, black light trap (Type no. 66496, USNM).

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BASIDIOMYCETES THAT DECAY JUNIPERS IN ARIZONA[1]

R. L. Gilbertson[2] and J. P. Lindsey[2]

Abstract.— Twenty-seven species of wood-rotting Basidiomycetes are reported to decay junipers in Arizona. A key to the species, descriptions, and line drawings of microscopic characters are provided. *Pyrofomes demidoffii*, *Daedalea juniperina*, *Poria rimosa*, and *Phellinus texanus* cause decay of heartwood in living trees. *Hyphoderma deserticola* Gilberts. et Linds. is described as new.

Species of the genus *Juniperus* of the Cupressaceae are among the most conspicuous members of the flora of Arizona. Five species occur in the state: *Juniperus deppeana* Steud. (alligator juniper), *Juniperus scopulorum* Sarg. (Rocky Mountain juniper), *Juniperus monosperma* (Engelm.) Sarg. (one-seed juniper), *Juniperus osteosperma* (Torr.) Little (Utah juniper), and *Juniperus communis* L. (common juniper). The first four species listed attain tree size and, with pinyon (*Pinus edulis* Engelm.), occupy a large area of Arizona in the pinyon-juniper woodland vegetation type from 4,500 to 7,500 feet in elevation (Little, 1968). However, junipers occur over a wider elevational range, from the upper desert grass vegetation type at 3,000 feet to the ponderosa pine forest at approximately 8,500 feet. The annual precipitation in the pinyon-juniper woodland is only 12-20 inches, most of which occurs in the summer rainy season in July and August and during a winter period in December or January. During the remainder of the year it is usually dry in the zones where the junipers are found, and conditions are unfavorable for the development of wood-rotting fungi.

A relatively small number of wood-rotting fungi have been found on junipers. This is probably due to the presence of fungistatic compounds in juniper wood. Species of oaks and pines, commonly associated with junipers and exposed to the same environmental conditions, are substrata for many wood-rotting fungi. Junipers are widely used in the Southwest for fence posts because of their high resistance to decay and their abundance in most areas. Junipers are also commonly used for fireplace wood.

Heartrot in living Arizona junipers is mainly attributed to four species in the Polyporaceae. These are *Pyrofomes demidoffii*, *Daedalea juniperina*, *Poria rimosa*, and *Phellinus texanus*. Fungi that decay dead branches on living trees include *Exidiopsis calcea*, *Lachnella alboviolascens*, and *Dendrothele incrustans*. A number of wood-rotting basidiomycetes are found on dead, fallen junipers, with *Gloeophyllum trabeum*, *Poria ferox*, *Coriolellus sepium*, and *Panus fulvidus* appearing to play major roles. *Poria apacheriensis* is commonly found on roots and the root crown region of dead standing junipers in southeastern Arizona and may cause a root-rot in living trees.

Microscopic characters were determined from freehand sections or crushed tissue in 4 percent KOH and phloxine and also in Melzer's reagent. Capitalized color names are from Ridgway (1912).

The only previous publication dealing specifically with fungi causing decay in junipers is that of Hedgcock and Long (1912). They discussed *Fomes juniperinus* (von Schrenk) Sacc. et Syd. and *Fomes earlei* (Murr.) Sacc. et D. Sacc. (now considered synonyms of *Pyrofomes demidoffii*) and *Fomes texanus*, included as *Phellinus texanus* in this paper.

Host indices listing decay fungi on junipers in the Southwest include those by Gilbertson, Martin, and Lindsey (1974) for Arizona and the U.S. Department of Agriculture host index (Anonymous, 1960). Shaw (1973) has provided a host index for fungi of the Pacific Northwest. He lists *Fomes juniperinus* (= *Pyrofomes demidoffii*) on *Juniperus communis* in Montana and *Polyporus hirtus* Quél. on *Juniperus scopulorum* in British Columbia. These are the only host-fungus relationships given by Shaw that are not recorded for the Southwest. The USDA host index lists *Fomes roseus* (Alb. et Schw. ex Fr.) Cke. and *Coniophora corrugis* Burt on juniper in Arizona, but we have not seen voucher specimens to support the records.

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Key to Fungi That Decay Junipers in Arizona

1. Hymenophore consisting of united tubes 2
Hymenophore smooth, hydnaceous, or lamellate 16

2(1). Tissue brown, becoming permanently blackened in KOH solution .... *Phellinus texanus*
Tissue white or pale colored, not permanently blackening in KOH solution 3

3(2). Basidiocarps centrally stipitate .... *Polyporus arcularius*
Basidiocarps sessile or resupinate 4

4(3). Basidiocarps with brick red context tissue .... *Pyrofomes demidoffii*
Basidiocarps with context not brick red 5

5(4). Basidiospores thick walled, dextrinoid in Melzer's reagent .... *Fomes fraxinophilus*
Basidiospores thin walled, not dextrinoid in Melzer's reagent 6

6(5). Basidiocarps always resupinate 7
Basidiocarps sessile or reflexed 11

7(6). Pore surface often rose pink; hyphae simple-septate, no clamp connections present .... *Poria tarda*
Pore surface white to pale buff; generative hyphae with clamp connections 8

8(7). Basidiospores subglobose to broadly ellipsoid .... *Poria apacheriensis*
Basidiospores cylindric to allantoid 9

9(8). Basidiospores allantoid; cystidia present .... *Poria rimosa*
Basidiospores cylindric; cystidia not present 10

10(9). Basidiospores 4-5.5 x 1.5-2 μm .... *Poria sinuosa*
Basidiospores 8-10 x 3-3.5 μm .... *Poria ferox*

11(6). Pores 1-4 per mm, circular to angular 12
Pores daedaloid or tubes splitting to form a lamellate hymenophore 14

12(11). Pore surface purplish; cystidia abundant, apically incrusted .... *Hirschioporus versatilis*
Pore surface cream colored; cystidia not present 13

13(12). Basidiospores 12-13 x 5-6.5 μm; pores 1-2 per mm .... *Coriolellus heteromorphus*
Basidiospores 10-14 x 3.5-4.5 μm; pores 2-4 per mm .... *Coriolellus sepium*

14(11). Pores large, daedaloid; tissue pale buff .... *Daedalea juniperina*
Pores regular, tubes splitting to form a lamellate hymenophore; tissue brown 15

15(14). Upper surface usually distinctly zonate with bright yellowish or reddish brown zones; hymenophore strongly lamellate .... *Gloeophyllum saepiarium*
Upper surface azonate or indistinctly zonate, dull brown; hymenophore poriod to lamellate .... *Gloeophyllum trabeum*

16(1). Basidiocarps stipitate; hymenophore radially lamellate .... *Panus fulvidus*
Basidiocarps sessile or resupinate; hymenophore smooth to hydnaceous 17

17(16). Basidiocarps cupulate, up to 2 mm wide .... *Lachnella alboviolascens*
Basidiocarps resupinate 18

18(17). Hymenophore smooth 19
Hymenophore hydnaceous 25

19(18). Basidia vertically septate .... *Exidiopsis calcea*
Basidia nonseptate 20

20(19). Hymenial surface olivaceous; basidiospores thick walled, dextrinoid in Melzer's reagent .... *Coniophora eremophila*
Hymenial surface not olivaceous; basidiospores thin walled, negative or amyloid in Melzer's reagent 21

21(20). Basidiospores amyloid in Melzer's reagent; acanthohyphidia and gloeocystidia present 22
Basidiospores negative in Melzer's reagent; acanthohyphidia and gloeocystidia not present 23

22(21). Basidiospores 6.5-8 x 4-5 μm; hymenial surface becoming bluish gray .... *Aleurodiscus lividocoeruleus*
Basidiospores 9.5-11.5 x 5.5-7 μm; hymenophore remaining pale buff .... *Aleurodiscus cerrusatus*

23(21). Basidiospores globose to subglobose; dendrohyphidia present .... *Dendrothele incrustans*
Basidiospores cylindric to ellipsoid; dendrohyphidia absent 24

24(23). Cystidia subulate, thin walled, 6-8 μm wide; aggregates of golden crystalline material present .... *Hyphoderma pallidum*
Cystidia cylindric, with a rooted base, thick walled, 10-12 μm wide; golden crystalline material absent .... *Hyphoderma deserticola*

25(18). Hymenophore papillate, papillae with an amber-colored, beadlike droplet at the apex .... *Dacryobolus sudans*
Hymenophore distinctly hydnaceous with cylindric or flattened teeth 26

26(25). Sagittate cysidia present .... *Hyphodontia arguta*
Sagittate cystidia not present .... *Hyphodontia spathulata*

Exidiopsis calcea (Pers.) Wells, Mycologia 53(4): 348. 1961.

Thelephora calcea Pers., Mycol. Eur. 1: 153. 1822.

Basidiocarps resupinate, thin, hard, arid-waxy, at first developing as small patches, then coalescing to become widely effused, cracking laterally to expose the substratum; hymenial surface white to grayish white, smooth, shining; margin minutely fimbriate, sometimes abrupt; subicular hyphae of two types, some narrow, branched, and sinuous, 1-1.5 μm diam, aseptate, others branched, with clamp connections, 3-5 μm diam (Fig. 1a), these giving rise to basidia; basidia (Fig. 1b) with a basal clamp connection, hypobasidia subglobose to ellipsoid, becoming longitudinally septate and four-celled at maturity, 12-15 x 15-20 μm, the four epibasidia to 55 μm long; basidiospores (Fig. 1c) cylindric, curved to slightly allantoid, smooth, hyaline, germinating by repetition, negative in Melzer's reagent, 14-20 x 6-8 μm.

Exidiopsis calcea decays dead branches of many trees and shrubs and occurs from the Sonoran Desert to high-elevation conifer forests. It is associated with a white rot.

Voucher specimen: E. R. Canfield, 71-131, on alligator juniper, Scotia Canyon, Huachuca Mts., Cochise Co., AZ (ARIZ).

Lachnella alboviolascens (Alb. et Schw. ex Fr.) Fr., Sum. Veg. Scand. p. 365. 1849.

Peziza alboviolascens Alb. et Schw. ex Fr., Syst. Myc. 2: 96. 1822.

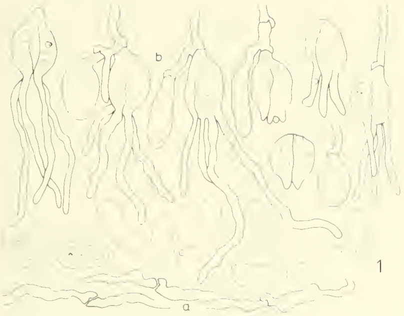


Fig. 1. *Exidiopsis calcea* (ERC 71-131), a, subicular hyphae; b, basidia; c, basidiospores.

Basidiocarps cupulate, gregarious, developing directly from the substratum with a small patch of basal white mycelium, separate or crowded together, to 1 mm diam, sessile; outer surface covered with a white, wooly-matted layer of hyphae; hymenial surface pale pinkish brown, smooth, obscured on dried specimens by the inrolled margin; hyphal system dimitic, generative hyphae of the outer layer (Fig. 2a) thick walled, hyaline, with occasional clamp connections, 5-7 μm diam, some with an extremely narrow, capillary lumen; skeletal hyphae (Fig. 2b) of outer layer thick walled, aseptate, to 7 μm diam; subhymenial hyphae moderately thick walled, with abundant clamp connections, 2-4 μm diam; basidia (Fig. 2c) broadly clavate, with thickened walls 50-90 μm long and 13-16 μm at the apex, four-sterigmate, the sterigmata 2-3 μm in basal diam; basidiospores (Fig. 2d) broadly ellipsoid, hyaline, negative in Melzer's reagent, 14-18 x 8.5-10 μm.

This fungus is common on dead branches of a number of southwestern desert shrubs and is associated with a brown rot.

Voucher specimen: RLG 10193, on oneseed juniper, Black Oak Cemetery, Canelo Rd., Santa Cruz Co., AZ (ARIZ).

CONIOPHORA EREMOPHILA Linds. et Gilberts., Mycotaxon 2: 86. 1975.

Basidiocarps fragile, easily separated, occurring in small patches or effused to 3 cm; hymenal surface smooth, becoming Brownish Olive from massed basidiospores as they mature; hymenial layer soft and floccose over a white arachnoid subiculum; margin with fine, white mycelial strands radiating from subiculum; subicular hyphae simple-septate, hyaline, often lightly incrusted, some (Fig. 3a) thin walled, 2-5 μm diam, others thin to thick walled (Fig. 3b), to 10 μm diam; cystidia none; basidia (Fig. 3c) utriform to clavate, usually sinuous, 40-60 x 6-10 μm, four-sterigmate, the sterigmata to 7 μm long; basidiospores (Fig. 3d) brownish olive in mass, pale yellow in KOH, cyanophilous, dextrinoid in Melzer's reagent, thick walled, ellipsoid to subglobose, 9-11 x 5-8.5 μm, with an apical germ pore and prominent peglike apiculus.

Coniophora eremophila has also been found on several Sonoran Desert trees and shrubs and is associated with a brown rot.

Voucher specimen: RLG 7400, on oneseed juniper, Gallinas Mts., Lincoln Co., NM (ARIZ).

ALEURODISCUS CERUSSATUS (Bres.) Hoehn. et Litsch., K. Acad. Wiss. Wien Math.-Nat. Kl. Sitzungsb. 116: 807. 1907.

Corticium cerussatum Bres., Fung. Trid. II. 37. 1892.

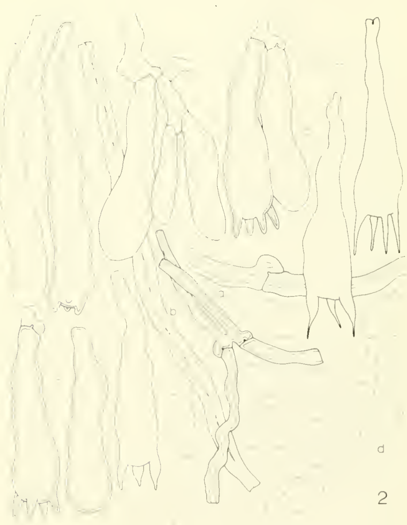


Fig. 2. *Lachnella alboviolascens* (RLG 10193), a, generative hyphae; b, skeletal hypha; c, basidia; d, basidiospores.

Basidiocarps in small patches, becoming confluent, effused, cracking deeply with age; hymenial surface cream to dull white; hyphal system monomitic, composed of contorted, thin walled hyphae (Fig. 4a) 2-4 μm diam, with abundant clamp connections; gloeocystidia (Fig. 4b) embedded, cylindric, sinuous, with refractive oily contents, some moniliform, 40-70 x 10-13 μm; weakly positive in sulphobenzaldehyde; acanthophyses (Fig. 4c) apically thick walled, thin walled at the base, cylindric, 30-55 x 3-4 μm; with a basal clamp connection; mature basidia (Fig. 4d) four-sterigmate, 5-9 x 45-60 μm; basidiospores (Fig. 4e) broadly cylindric to ellipsoid, thin walled, smooth, amyloid in Melzer's reagent, mostly collapsed or fragmented, 9-11 x 5-7 μm.

Aleurodiscus cerussatus grows on dead branches of other shrubs and trees in the Southwest. It is associated with a white rot.

Voucher specimen: RLG 8551, on oneseed juniper, Chiricahua Nat. Monument, Chiricahua Mts., Cochise Co., AZ (ARIZ).

ALEURODISCUS LIVIDOCOERULEUS (Karst.) Lemke, Can. J. Bot. 42: 252. 1964.

Corticium lividocoeruleum Karst., Not. Sälsk. Faun. et Flor. Fenn. Förh. 9: 570. 1868.

Basidiocarps resupinate, originating as small, separate patches, then becoming confluent and widely effused, waxy; margin abrupt and fertile; hymenial surface cream colored or Pale Pinkish Buff to bluish gray (Light Neutral Gray to Dark Plumbeus), often rimose with age; hyphal system monomitic; subicular hyphae (Fig. 5a) thin walled, with clamp connections, 3-6 μm diam; gloeocystidia (Fig. 5b) abundant, positive in sulphobenzaldehyde, embedded or slightly projecting, some moniliform or mammillate, 20-90 x 6-13 μm; acanthophyses (Fig. 5c) abundant, aculeate over the terminal portion, thin to thick walled at the apex, with a basal clamp connection, 15-30 x 3-7 μm; basidia (Fig. 5d) clavate, 40-50 x 10-11 μm, sterigmata not seen; basidiospores (Fig. 5e) broadly cylindric to ellipsoid, hyaline, smooth, amyloid in Melzer's reagent, thin walled and collapsing readily, 6-8 x 3.5-5 μm.

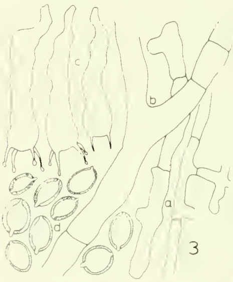
This fungus occurs throughout the Rocky Mountain region on many conifers. It is associated with a white rot.

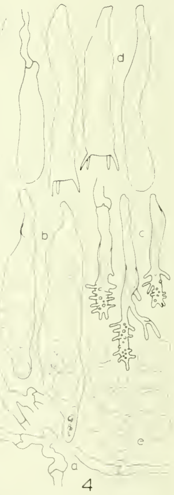
Voucher specimens: RLG 10777, on alligator juniper, Turkey Creek, Chiricahua Mts., Cochise Co., AZ; ERC 71-234, on alligator juniper, General Hitchcock Picnic Area, Santa Catalina Mts., Pima Co., AZ (ARIZ).

DENDROTHELE INCRUSTANS (Lemke) Lemke, Persoonia 3: 366. 1965.

Aleurocorticium incrustans Lemke, Can. J. Bot. 42: 739. 1964.

Basidiocarps small, usually in patches up to 5 mm wide, sometimes confluent; margin abrupt, fertile; hymenial surface smooth, white to Cartridge Buff or cinereous, rimose on drying; subicular hyphae (Fig. 6a) slender, with frequent branching, with inconspicuous clamp connections, 1-2.5 μm diam; cystidia absent; hyaline





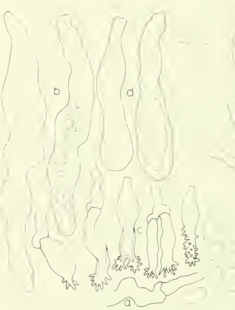


Fig. 3. *Coniophora eremophila* (RLG 7400), a, narrow subicular hyphae; b, broad subicular hypha; c, basidia; d, basidiospores.

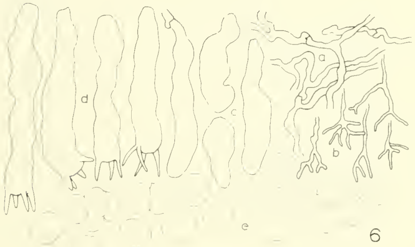
Fig. 4. *Aleurodiscus cerrusatus* (RLG 8551), a, subicular hyphae; b, gloeocystidia; c, acanthophyses; d, basidia; e, basidiospores.

Fig. 5. *Aleurodiscus lividocoeruleus* (RLG 10777), a, subicular hypha; b, gloeocystidia; c, acanthophyses; d, immature basidia; e, basidiospores.

dendrohyphidia (Fig. 6b) abundant in hymenial region, ultimate branches 1 μm diam or less; basidia (Fig. 6d) clavate to cylindric, some swollen at the base, developing from imbedded basidioles (Fig. 6c), 30-60 x 8-10 μm, four-sterigmate, with a basal clamp connection; basidiospores (Fig. 6e) hyaline, smooth, negative in Melzer's reagent, globose to subglobose, 9-11 x 8-9.5 μm, sometimes adhering in groups of two to four.

Dendrothele incrustans apparently utilizes bark tissue as a substratum. It also occurs on bark of several other southern Arizona trees, including oaks and Arizona madrone (*Arbutus arizonica* (Gray) Sarg.). Lemke (1964) reports this fungus (as *Aleurocorticium incrustans*) from several localities in the Pacific Northwest, but it has not been reported previously from the Southwest.

Voucher specimen: RLG 10020, on bark of living alligator juniper, Turkey Creek, Chiricahua Mts., Cochise Co., AZ (ARIZ).



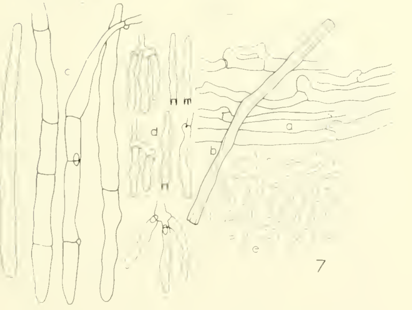


Fig. 6. *Dendrothele incrustans* (RLG 10020). a, subicular hyphae; b, dendrohyphidia; c, basidioles; d, mature basidia; e, basidiospores, some in pairs and tetrads.

Fig. 7. *Dacryobolus sudans* (RLG 9319, 9944, and 10322). a, subicular hyphae; b, fragment of thick-walled hypha; c, cystidia; d, basidia; e, basidiospores.

Dacryobolus sudans (Fr.) Fr., Summa. Veg. Scand. p. 404. 1849.

Hydnum sudans Fr., Syst. Myc. 1: 425. 1821.

Basidiocarps resupinate, adnate, effused up to 6 cm; hymenial surface papillose, Cream Color to Warm Buff; papillae hemispherical and wartlike to conical, each terminated by a drop of amber, viscous liquid that dries to form a beadlike apex; papillae also appearing as small craters where the exudate has broken away; subicular hyphae (Fig. 7a) thin to thick walled, with clamp connections, fragments of thick walled hyphae (Fig. 7b) appearing aseptate, 1.5-5 μm diam; cystidia (Fig. 7c) thin walled, nonseptate or with clamps and simple septa, clustered at apices of papillae, 70-90 x 3-6 μm; basidia (Fig. 7d) narrowly clavate, 20-25 x 3-3.5 μm, four-sterigmate, with a basal clamp connection; basidiospores (Fig. 7e) narrowly allantoid, hyaline, smooth, negative in Melzer's reagent, 5-7 x 1-1.5 μm.

Dacryobolus sudans is associated with a distinctive brown cubical pocket rot.

Voucher specimen: RLG 9944, on one-seed juniper, Sycamore Canyon, Atascosa Mts., Santa Cruz Co., AZ (ARIZ).

Hyphoderma deserticola Gilberts. et Linds., sp. nov.

Basidiocarpus effusus, mollis; hymenium laevis, bubalinus, cystidiis; hyphis systematis monomitico; hyphis subiculis tenuitunicatis, 3-5 μm diam; hyphis fibulatis; cystidia numerosa, subulata, 90-125 x 6-13 μm, base ramosa, radicata; basidia clavata, constrictione media, 20-30 x 6-7 μm, 4 sterigmatibus; basidiosporae hyalinae, laeves, non amyloideae, 6-7 x 3-4 μm. HOLOTYPUS: in ligno *Juniperus deppeana* Steud., Gardner Canyon, Santa Rita Mts., Santa Cruz County, AZ, USA, leg. R. L. Gilbertson, no. 10921; in herb. Nat. Fungus Collections, Beltsville, MD, USA (BPI).

Basidiocarps effused, in small, confluent patches, soft, easily separated; hymenial surface smooth, Light Buff to Pale Pinkish Buff, becoming rimose on drying, cystidiate under a 30X lens, cystidia appearing pale golden or amber due to apical incrustation; hyphal system monomitic; subicular hyphae (Fig. 8a) thin to moderately thick walled, closely septate, with clamp connections at all septa, 3-5 μm diam; cystidia (Fig. 8b) abundant, subulate, thin to moderately thick walled, many

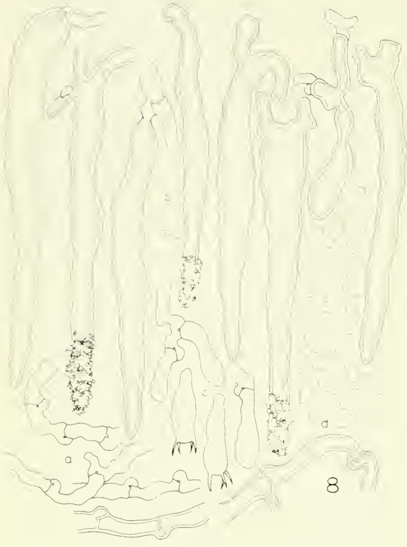


Fig. 8. *Hyphoderma deserticola* (RLG 10921), a, subicular hyphae; b, cystidia; c, basidia; d. basidiospores.

with a branched, rooted base, 90-125 x 6-13 μm, most apically incrusted with fine, pale golden crystals that dissolve readily in KOH; basidia (Fig. 8c) clavate, with a median constriction, 20-30 x 6-7 μm, four-sterigmate, occurring in candelabrums, with a basal clamp connection; basidiospores (Fig. 8d) hyaline, smooth, cylindric-ellipsoid, negative in Melzer's reagent, 6-7 x 3-4 μm.

Basidiocarps of *Hyphoderma deserticola* are macroscopically and microscopically similar to those of *H. argillaceum* (Bres.) Donk. Cystidia of *H. deserticola* are more thick walled and less swollen at the base than those of *H. argillaceum* and many are branched and rooted at the base. The apical incrustation on the cystidia is best seen in water mounts and dissolves rapidly in KOH. Basidiospores of *H. argillaceum* are wider (4-5 μm) than those of *H. deserticola*, appearing more ellipsoid than cylindric. *Hyphoderma macedonicum* (Bres.) Donk, as described by Eriksson and Ryvarden (1975), is also similar but has thin-walled, nonrooted cystidia and narrower spores (2-2.5 μm) than *H. deserticola*.

Voucher specimen: RLG 10921, on alligator juniper, Gardner Canyon, Santa Rita Mts., Santa Cruz Co., AZ (TYPE).

HYPHODERMA PALLIDUM (Bres.) Donk, Fungus 27: 15. 1957.

Corticium pallidum Bres., Fung. Trid. 2: 59. 1898.

Basidiocarps effused up to 10 cm, soft, thin; hymenial surface Tilluel-Buff to Pale Vinaceous-Fawn, smooth, speckled with golden brown under a 30X lens; margin thinning out, fertile; hyphal system monomitic; subicular hyphae (Fig. 9a) with clamp connections, 2.5-4 μm diam; spherical to irregularly shaped masses of golden brown crystalline material (Fig. 9d) abundant throughout subiculum, to 30 μm wide; cystidia (Fig. 9b) narrowly subulate, thin walled, not incrusted, 40-50 μm long and 6-8 μm wide at the swollen base; basidia (Fig. 9c) clavate, four-sterigmate, 25-35 x 6-7 μm, with a basal clamp connection; basidiospores (Fig. 9e) hyaline, smooth, slightly curved, cylindric, negative in Melzer's reagent, 8-11 x 3-4 μm.

Hyphoderma pallidum is associated with a white rot of conifer slash in the Southwest.

Voucher specimen: RLG 10778, on alligator juniper, Turkey Creek, Chiricahua Mts., Cochise Co., AZ (ARIZ).

HYPHODONTIA ARGUTA (Fr.) J. Erikss., Symb. Bot. Upsal. 16: 1, p. 104. 1958.

Hydum argutum Fr., Syst. Myc. 1: 424. 1821.

Basidiocarps becoming widely effused, hymenial surface hydnaceous, Light Buff to Pinkish Buff, the teeth usually crowded, cylindric and tapering at the apex, simple or branched, up to 3 mm long, the apices finely tomentose or fimbriate; subiculum cream colored to pale buff, very soft and thin; hyphal system monomitic; subicular hyphae (Fig. 10a) thin walled, with frequent branching, with abundant clamp connections, 2-3 μm diam; cystidia of two types, some (Fig. 10c) sagittate, apically incrusted, 15-30 μm long, projecting up to 18 μm, 5-6 μm diam at the swollen base, slender, stalklike part 1.5-2 μm diam, incrusted apex about 2.5 μm diam, other cystidia (Fig. 10b) not incrusted, with slight terminal or intercalary swellings, often with clamp connections, thin walled, 40-50 x 3-6 μm and projecting to 25 μm; basidia (Fig. 10d) clavate, with a median constriction, four-sterigmate, 10-21 x 4-5 μm; basidiospores (Fig. 10e) ovoid to ellipsoid, hyaline, smooth, negative in Melzer's reagent, 4-6 x 2.5-4 μm.

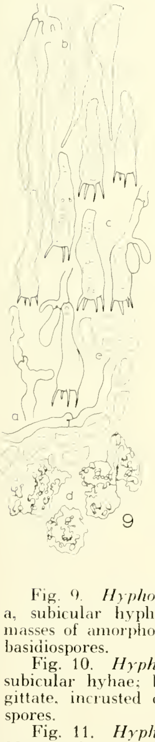
Hyphodontia arguta has been found on both conifers and hardwoods in the Southwest and is associated with a white rot.

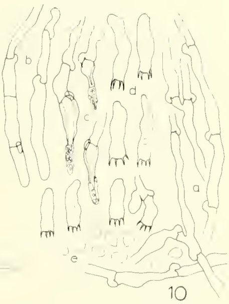
Voucher specimen: RLG 8325, on alligator juniper, Carr Canyon, Huachuca Mts., Cochise Co., AZ (ARIZ).

HYPHODONTIA SPATHULATA (Schrad. ex Fr.) Parm., Conspect. Syst. Cort. p. 123. 1968.

Hydnum spathulatum Schrad. ex Fr., Syst. Myc. 1: 423. 1821.

Basidiocarps becoming widely effused; hymenial surface hydnaceous, cream colored to Light Buff, the teeth cylindric to flattened and tending to be confluent, forming elongated ridges; hyphal system monomitic; subicular hyphae (Fig. 11a) thin to moderately thick walled, with abundant clamp connections, with frequent branching and irregular swellings and constrictions, 2-4 μm diam; cystidia (Fig. 11b) capitate, 25-30 x 3-4 μm, slightly projecting, also hyphoid end cells tufted at apices of teeth, these lightly incrusted; basidia (Fig. 11c) clavate with a median constriction, 15-17 x 5-6 μm, four-sterigmate; basidiospores (Fig. 11d) ovoid to subglobose, hyaline, negative in Melzer's reagent, smooth, 4-5 x 3-4 μm.





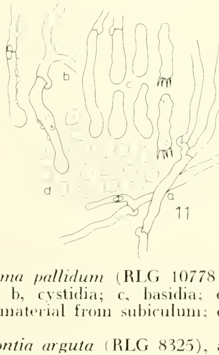


Fig. 9. *Hyphoderma pallidum* (RLG 10778), a, subicular hyphae; b, cystidia; c, basidia; d, masses of amorphous material from subiculum; e, basidiospores.

Fig. 10. *Hyphodontia arguta* (RLG 8325), a, subicular hyhae; b, nonincrusted cystidia; c, sagittate, incrusted cystidia; d, basidia; e, basidiospores.

Fig. 11. *Hyphodontia spathulata* (RLG 9795, 9949, and 10131), a, subicular hyphae; b, capitate cystidia; c, basidia; d, basidiospores.

Hyphodontia spathulata is associated with a white rot of both conifers and hardwoods in the Southwest.

Voucher specimen: RLG 10131, on alligator juniper, Parker Canyon, Huachuca Mts., Santa Cruz Co., AZ (ARIZ).

PHELLINUS TEXANUS (Murr.) Gilberts. et Canf., Mycologia 65: 1304. 1972.

Pyropolyporus texanus Murr., N. Amer. Fl. 9: 104. 1908.

Basidiocarps perennial, sessile, ungulate, up to 15 cm wide; upper surface at first pale brown, matted-tomentose, becoming blackened and deeply rimose with age and weathering, sulcate; margin rounded, pale brown and tomentose; pore surface pale brown (Buckthorn Brown to Mummy Brown), smooth, the pores 4-6 per mm; dissepiments finely tomentose, entire; context hard and woody, yellowish brown, appearing mottled with streaks of paler tissue; tube layers stratified, Buckthorn Brown, becoming stuffed with light-colored mycelium; sections permanently darkening in KOH solution; some contextual hyphae thin walled and hyaline to yellowish, with occasional septa and rare branching, 2-5 μm diam (Fig. 12a), others thick walled, yellowish brown, aseptate, with rare branching, 3-5 μm diam (Fig. 12b); hyphae in the pale colored areas with a parallel arrangement, easily separated, hyphae in the darker areas densely interwoven, contorted, difficult to separate; tramal hyphae interwoven, pale yellowish, with slightly thickened walls and occasional septa, 2-4 μm diam; setae (Fig. 12d) few, slightly thick walled to thick walled, with an inflated base to 10 μm diam and a slender apical portion, 25-60

Fig. 12. *Phellinus texanus* (RLG 6959), a, thin-walled contextual hyphae; b, thick-walled contextual hyphae; c, thin-walled cystidioid hyphal ends; d, setae; e, basidia; f, basidiospores.

μm long; setae apparently developing from hyaline, thin walled cystidioid hyphal ends (Fig. 12c) similar in shape and size to the setae and common in all sections; basidia (Fig. 12e) broadly clavate to ovoid, four-sterigmate, 17-25 x 8.5-12 μm, the sterigmata slender, to 4 μm long; basidiospores (Fig. 12f) subglobose, hyaline, strongly dextrinoid in Melzer's reagent and with distinctly thickened walls when mature, 7-9 x 6.5-9 μm.

Phellinus texanus occurs on many Sonoran Desert trees and shrubs including cacti, and causes a white heartrot of living plants.

Voucher specimens: RLG 6959, on alligator juniper, Sponsellor Lake Rd., Navajo Co., AZ; RLG 7406, on one-seed juniper, Gallinas Mts., Lincoln Co., NM; RLG 8042, on Rocky Mountain juniper, Doc Long Picnic Area, Sandia Mts., Bernalillo Co., NM; P. D. Keener 74, on alligator juniper, Mingus Mt., Yavapai Co., AZ; K. J. Martin 483, on alligator juniper, Rucker Campground, Chiricahua Mts., Cochise Co., AZ (ARIZ); W. H. Long, 327, TX (TYPE) (NY).

CORIOLELLUS HETEROMORPHUS (Fr.) Bond. et Sing., Ann. Myc. 39: 60. 1941.

Daedalea heteromorpha Fr., Syst. Myc. 1: 340. 1821.

Basidiocarps annual, sessile, effused-reflexed, or resupinate; upper surface on reflexed specimens cream colored to pale brownish, glabrous to finely tomentose; pore surface Light Buff to Pinkish Buff; pores regular to slightly daedaloid, 1-2 per mm, or in some specimens mostly over 1 mm diam; dissepiments thick and tomentose at first, becoming thin and splitting with age; margin thinning out or abrupt, tomentose; context very thin, pale buff; tube layer concolorous with context; hyphal system dimitic; generative hyphae (Fig. 13a) hyaline, thin to thick walled, with abundant clamp connections, 3-4 μm diam; skeletal hyphae (Fig. 13b) hyaline, thick walled, aseptate, with occasional branching, 3-7 μm diam; cystidia none; basidia (Fig. 13c) clavate, four-sterigmate, 30-40 x 9-11 μm, with a basal clamp connection; basidiospores (Fig. 13d) hyaline, broadly cylindric, narrowed and curved near the apiculus, smooth, negative in Melzer's reagent, 10-13 x 5-7 μm.

Coriolellus heteromorphus causes a brown cubical rot, usually of conifers. Thin, white mycelial felts develop in the shrinkage cracks of the decayed wood. Resupinate specimens with large pores may be confused with *Daedalea juniperina*. The later can be distinguished by its much smaller spores and basidia.

Voucher specimens: RLG 9306, 9945, and 9952, on one-seed juniper, Sycamore Canyon, Atascosa Mts., Santa Cruz Co., AZ (ARIZ).

CORIOLELLUS SEPIUM (Berk.) Murr., Torrey Bot. Club Bull., 32: 481. 1905.

Trametes sepium Berk., London J. Bot. 6: 322. 1847.

Basidiocarps annual, sessile, effused-reflexed, or occasionally resupinate, pilei solitary or imbricate, dimidiate to elongate, to 25 x 4 x 2 cm; surface of the pileus Light Buff to Mummy Brown or blackening with age, glabrous or finely

Fig. 13. *Coriolellus heteromorphus* (RLG 9952), a, generative hyphae; b, skeletal hyphae; c, basidia; d, basidiospores.

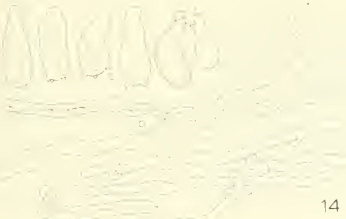


Fig. 14. *Coriolellus sepium* (RLG 10129), a, contextual generative hyphae; b, contextual skeletal hyphae; c, basidia; d, basidiospores.

tomentose, azonate, shallowly sulcate, smooth or slightly rugose; margin concolorous, rounded, fertile or narrowly sterile below; pore surface Cinnamon Buff to Buckthorn Brown, the pores circular to angular, 2-3 per mm, the dissepiments thick, entire, eventually becoming lacerate; context ivory, azonate, corky, to 4 mm thick; the tube layer concolorous and continuous with context, to 1 cm thick; odor sometimes fragrant; hyphal system dimitic; contextual generative hyphae (Fig. 14a) hyaline in KOH, mostly thin walled, rarely branched, with abundant clamp connections, 2.5-5.5 μm diam; contextual skeletal hyphae (Fig. 14b) thick walled, aseptate, 3-5.5 μm diam; tramal hyphae similar; cystidia none; basidia (Fig. 14c) clavate, four-sterigmate, 20-25 x 8-10 μm; basidiospores (Fig. 14d) hyaline, negative in Melzer's reagent, cylindric, 9.5-14 x 3-4 μm.

Coriolellus sepium is associated with a brown cubical rot with thin, arachnoid mycelial felts.

Voucher specimens: RLG 7261, on alligator juniper, Rucker Canyon, Chiricahua Mts., Cochise Co., AZ; RLG 10045, on juniper post, Washington Camp, Patagonia Mts., Santa Cruz Co., AZ; RLG 10048, on alligator juniper, Montezuma Pass, Huachuca Mts., Cochise Co., AZ; RLG 10198, on juniper post, Sunnyside, Cochise Co., AZ; RLG 10129, on alligator juniper, Parker Canyon Lake, Cochise Co., AZ; RLG 10838, on alligator juniper, Indian Creek, Animas Mts., Hidalgo Co., NM; ERC 70-1, on alligator juniper, Rustler Park, Chiricahua Mts., Cochise Co., AZ; ERC 71-129, on alligator juniper, Scotia Canyon, Huachuca Mts., Cochise Co., AZ (ARIZ).

DAEDALEA JUNIPERINA Murr., N. Amer. Fl. 9: 125. 1908.

Basidiocarps annual or perennial, effused-reflexed or resupinate; pilei solitary or imbricate, often laterally fused, to 5 x 10 x 9 cm; surface of the pileus weathering Light Buff to Cinnamon Buff, to gray or blackish, indistinctly zonate, becoming glabrous and incrusted; pore surface Light Buff, rough, pores large, daedaloid, often more than 1 mm diam; dissepiments thick, entire, splitting with age to form lamellae or spines; context yellowish ivory, soft-corky, faintly zonate, to 2 cm thick; tube layers concolorous and continuous with context, to 6 cm long; hyphal system dimitic; contextual generative hyphae (Fig. 15a) thin walled, with rare branching, with abundant clamp connections, 3-6 μm diam; contextual skeletal hyphae (Fig. 15b) hyaline in KOH, thick walled, with rare branching, aseptate, 3-7 μm diam; tramal hyphae similar; cystidia none; basidia (Fig. 15c) clavate, 20-25 x 6-7 μm, four-sterigmate; basidiospores

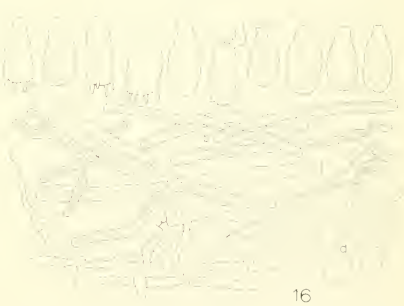


Fig. 15. *Daedalea juniperina* (JPL 328, RLG 10604). a, contextual generative hyphae; b, contextual skeletal hyphae; c, basidia; d, basidiospores.

Fig. 16. *Fomes fraxinophilus* (ERC 71-25), a, subicular generative hyphae; b, subicular skeletal hyphae; c, basidia; d, basidiospores.

(Fig. 15d) hyaline, negative in Melzer's reagent, smooth, cylindric, 6.5-9 x 2.5-3.5 μm.

Daedalea juniperina is associated with a brown cubical heartrot of living junipers. Thick, buff colored mycelial felts develop in shrinkage cracks of decayed wood.

Voucher specimens: RLG 6940, on one-seed juniper, Salt River Canyon, Gila Co., AZ; RLG 9945 and ERC 71-26, on one-seed juniper, Sycamore Canyon, Atascosa Mts., Santa Cruz Co., AZ; P. D. Keener, on alligator juniper, Mingus Mt., Yavapai Co., AZ; RLG 10604, on Utah juniper, Seegmuller Mt., Mohave Co., AZ; JPL 328, on alligator juniper, Rucker Canyon, Chiricahua Mts., Cochise Co., AZ; KJM 335, on one-seed juniper, Canyon del Oro, Santa Catalina Mts., Pinal Co., AZ (ARIZ).

FOMES FRAXINOPHILUS (Pk.) Cke., Grevillea 15: 51. 1886.

Polyporus fraxinophilus Pk., Bot. Gaz. 7: 43-44. 1882.

Basidiocarps perennial, resupinate, effused to 6 cm; pore surface Pale Ochraceous Buff to Pinkish Buff, the pores 3-4 per mm; dissepiments thick, minutely tomentose; margin narrowly sterile, 0.5 mm wide, Light Buff; subiculum pale buff, to 1.5 mm thick; hyphal system dimitic; generative hyphae (Fig. 16a) in subiculum thin walled, 2-3 μm diam, with inconspicuous clamp connections, these more apparent in marginal tissue; subicular skeletal hyphae (Fig. 16b) hyaline, moderately thick walled to thick walled, with occasional branching, aseptate or rarely with simple septa, 2.5-5 μm diam; tramal hyphae similar to subicular skeletal hyphae but mostly 2-3 μm diam; cystidia none; basidia (Fig. 16c) broadly clavate, four-sterigmate, 20-25 x 9-11 μm; basidiospores (Fig. 16d) broadly ellipsoid to subglobose, truncate at the apex, hyaline, dextrinoid in Melzer's reagent, 9-10.5 x 6.5-8 μm, thick walled at maturity with a germ pore at the truncate apex.

Fomes fraxinophilus causes a white heartrot of living trees and is common in southern Arizona on *Fraxinus velutina* Torr. (Arizona ash). Small resupinate basidiocarps are also commonly found on ash. Clamp connections of *F. fraxinophilus* are abundant and conspicuous in dikaryotic cultures of the fungus but are difficult to discern in basidiocarp tissue.

Voucher specimens: ERC 71-25, on one-seed juniper, Sycamore Canyon, Atascosa Mts., Santa Cruz Co., AZ; J. L. Lowe 9091, on one-seed juniper, Silver Creek Rd., Chiricahua Mts., Cochise Co., AZ (ARIZ).

GLOEOPHYLLUM SAEPIARIUM (Wulf. ex Fr.) Karst., Finl. Hattsv. 2: 80. 1879.

Daedalea sepiaria Wulf. ex. Fr., Syst. Myc. 1: 333. 1821.

Basidiocarps annual, effused-reflexed, sessile, or occasionally resupinate; upper surface Warm Sepia to Bister or blackening, hirsute to coarsely strigose, concentrically zonate; lower surface Sudan Brown to Amber Brown, pores present at the margin of some specimens, but tubes typically splitting to form a radially lamellate hymenophore; context Honey Yellow to Clay Color, darkening to Sepia, azonate, up to 4 mm thick; hyphal system dimitic; contextual generative hyphae (Fig. 17a) hyaline, thin walled, with abundant clamp connections, 3-5 μm diam; contextual skeletal hyphae (Fig. 17b) thick walled, pale yellowish brown, aseptate, with occasional branching, 2.5-5 μm diam; cystidia (Fig. 17c) thin to thick walled, cylindric, not incrusted, to 85 μm long and 2.5-6 μm diam; basidia (Fig. 17d) narrowly clavate, with a greatly elongated base, 60-80 x 7-8 μm; basidiospores hyaline, smooth, cylindric, slightly curved, negative in Melzer's reagent, 8.5-11 x 3-4 μm.

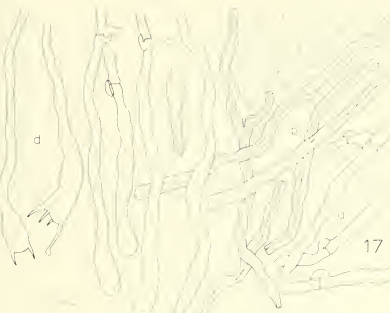
Gloeophyllum saepiarium causes a brown cubical rot of conifers and hardwoods in Arizona but is rarely found on juniper.

Voucher specimen: RLG 10918, on alligator juniper, Gardner Canyon, Santa Rita Mts., Santa Cruz Co., AZ (ARIZ).

GLOEOPHYLLUM TRABEUM (Pers. ex Fr.) Murr., N. Amer. Fl. 9: 129. 1908.

Daedalea trabea Pers. ex Fr., Syst. Myc. 1: 335. 1821.

Basidiocarps annual, sessile, effused-reflexed or occasionally resupinate in early stages of development; pilei dimidiate to elongated, often imbricate and confluent; upper surface yellowish - brown, weathering to tan or grayish, tomentose and be-



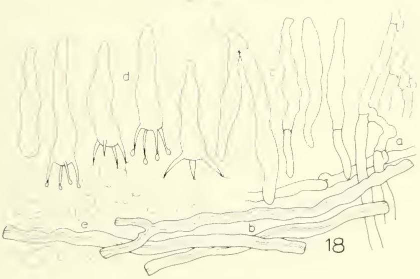


Fig. 17. *Gloephyllum saepiarium* (RLG 10918), a. contextual generative hyphae; b. contextual skeletal hyphae; c. cystidia; d. basidia; e. basidiospores.

Fig. 18. *Gloephyllum trabeum* (RLG 10128), a. contextual generative hyphae; b. contextual skeletal hyphae; c. cystidia; d. basidia; e. basidiospores.

coming glabrous, faintly zonate; lower surface pale brownish, poroid at first and in some specimens remaining poroid with pores 1-3 per mm, radially elongated, in others becoming radially lamellate by splitting of dissepiments; context pale brown, soft-felty, azonate, up to 12 mm thick; tube layer or lamellae pale brown, up to 4 mm thick; hyphal system dimitic; contextual generative hyphae (Fig. 18a) hyaline, thin walled, with abundant clamp connections, 2-3.5 μm diam; contextual skeletal hyphae (Fig. 18b) pale yellowish brown, thick walled, aseptate, with rare branching, 3-5.5 μm diam; tramal hyphae similar; cystidia (Fig. 18c) cylindric, thin walled, 35-50 x 3-5 μm; basidia (Fig. 18d) clavate, four-sterigmate, 30-45 x 5-7 μm; basidiospores (Fig. 18e) cylindric, hyaline, smooth, negative in Melzer's reagent, 7.5-9 x 3-3.5 μm.

Gloeophyllum trabeum is associated with a brown cubical rot. Mycelial felts do not develop in the decayed wood. *G. trabeum* is the most common wood-rotting fungus on dead fallen junipers in southern Arizona and is also found as a wood-rotting fungus on houses in Tucson.

Voucher specimens: RLG 10128, on alligator juniper, Parker Lake, Huachuca Mts., Cochise Co., AZ; RLG 10132, on alligator juniper, Sunnyside, Huachuca Mts., Cochise Co., AZ; RLG 10204, on alligator juniper, Scotia Canyon, Huachuca Mts., Cochise Co., AZ (ARIZ).

HIRSCHIOPORUS VERSATILIS (Berk.) Imazeki, J. Jap. Bot. 20: 288. 1945.

Trametes versatilis Berk., Hooker's J. Bot. 1: 150. 1842.

Basidiocarps resupinate to effused-reflexed, annual; pore surface purplish when fresh, dull purplish brown on age and drying, the pores circular to angular, 1-2 per mm; hyphal system dimitic; subicular generative hyphae (Fig. 19a) thin walled, 2-3.5 μm diam, with inconspicuous clamp connections; tramal hyphae similar; contextual skeletal hyphae (Fig. 19b) hyaline, thick walled, aseptate or with rare clamp connections, with rare branching, 2.5-5 μm diam; cystidia (Fig. 19c) abundant, fusoid, capitately incrusted, 20-30 x 3-5 μm; basidia (Fig. 19d) clavate, four-sterigmate, 14-17 x 5-6 μm; basidiospores (Fig. 19e) cylindric, hyaline, negative in Melzer's reagent, 5.5-8 x 2-2.5 μm.

Hirschioporus versatilis causes a white pocket rot and is apparently rare in the Southwest.

Voucher specimens: W. H. Long and G. G. Hedgcock, F. P. 9876, on one-seed

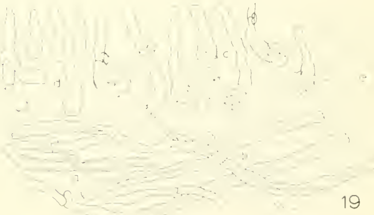


Fig. 19. *Hirschioporus versatilis* (JLL 11454), a. contextual generative hyphae; b. contextual skeletal hyphae; c. capitately incrusted cystidia; d. basidia; e. basidiospores.

juniper, Magdalena, NM, Type of *Trametes rubricosa* Bres. (BPI); G. G. Hedgcock, F. P. 18496, on one-seed juniper. Gila Nat. Forest, NM, determined as *T. rubricosa* by Bresadola (BPI); G. G. Hedgcock and W. H. Long, F. P. 10410, on one-seed juniper, Mogollon, NM (BPI); W. H. Long, 12704, on one-seed juniper, Winona, Coconino Co., AZ (ARIZ).

POLYPORUS ARCULARIUS Batsch ex Fr., Syst. Myc. 1: 342. 1821.

Basidiocarps annual, centrally stipitate; pilei circular, solitary, up to 2.5 cm diam and 0.3 cm thick; surface of the pileus straw colored to dark brown, azonate, glabrous, smooth to rugose; margin ciliate, acute, sterile below; stripe central, concolorous with pileus, glabrous, up to 3.5 cm long and 0.4 cm thick; pore surface cream colored to buff, dull, rough, the pores large, hexagonal, radially aligned, 1-2 per mm, the dissepiments thin, becoming lacerate; context whitish to buff, azonate, tough, less than 1 mm thick; tube layer concolorous and continuous with context, up to 2 mm thick; hyphal system dimitic; generative hyphae (Fig. 20b) hyaline in KOH, thin walled, often branched, with abundant clamp connections, 2.5-5 μm diam; skeletal hyphae (Fig. 20c, Fig. 20d) thick walled, aseptate, with occasional branching, 2-11 μm diam; tramal hyphae similar, not readily separable; hyphae on pileus surface (Fig. 20a) slender, thin walled, with clamp connections, 1-1.5 μm diam; basidia (Fig. 20e) four-sterigmate, clavate, 25-35 x 5-6 μm; cystidia none; basidiospores (Fig. 20f) hyaline, negative in Melzer's reagent, smooth, cylindric, straight or slightly curved, 7-9 x 2.5-3.5 μm.

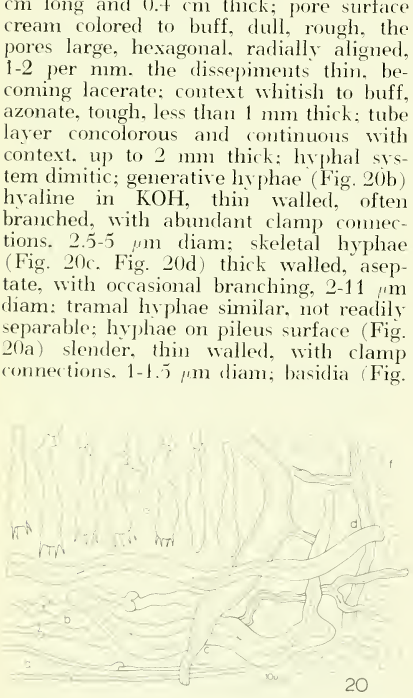


Fig. 20. *Polyporus arcularius* (JPL 278 and RLG 7903). a. hyphae from pileus surface; b. generative hyphae; c. broad skeletal hyphae; d. narrow skeletal hyphae; e. basidia; f. basidiospores

Polyporus arcularius causes a white rot and is especially common on dead oak wood throughout the oak woodland vegetation zone in southern Arizona. It is occasionally found on other substrata. This report is based on a field observation of *P. arcularius* on one-seed juniper at Sunnyside, Huachuca Mts., Cochise Co., AZ by RLG.

PORIA APACHERIENSIS Gilberts. et Canf., Mycologia 65: 1117. 1973.

Basidiocarps annual, effused up to 10 cm, adnate, soft-fibrous; pore surface white to Cream Color or Light Buff; sterile margin tomentose; pores circular to daedaloid, up to 1 μm diam, mostly 2-3 per mm; tube layer soft-fibrous, white to cream colored, up to 2 mm thick; subiculum soft, white, less than 0.5 mm thick; hyphal system monomitic; subicular hyphae (Fig. 21a) with abundant clamp connections, thin to moderately thick walled, with occasional branching, 2-4 μm diam; tramal hyphae similar, incrusted at dissepiment edges; cystidia thin walled, of two types, some acicular or cylindric (Fig. 21b), smooth to lightly incrusted, 45-60 x 2.5-5 μm, others capitate (Fig. 21c), 3-5 μm diam with swollen apex up to 8 μm diam, 40-50 μm long; basidia (Fig. 21d) with a median constriction, four-sterigmate, 18-30 x 6-7 μm; basidiospores (Fig. 21e) hyaline, smooth, negative in Melzer's reagent, broadly ellipsoid to subglobose, 5-6.5 x 4.5-5.5 μm.

Poria apacheriensis occurs on a number of Sonoran Desert plants, including the Saguaro cactus, *Carnegiea gigantea* (Engelm.) Britt. et Rose (Lindsey and Gilbertson, 1975), and causes a white rot. It fruits around the base of recently killed junipers at the ground line, suggesting it may cause a root rot in living trees.

Voucher specimens: RLG 10047 and ERC 184, on alligator juniper, Montezuma Pass, Cochise Co., AZ (ARIZ).

PORIA FEROX Long et Baxter, Papers Mich. Acad. Sci. 25: 149. 1940.

Basidiocarps perennial, becoming widely effused; pore surface Cartridge Buff to Pinkish Buff or Pale Orange Yellow, the

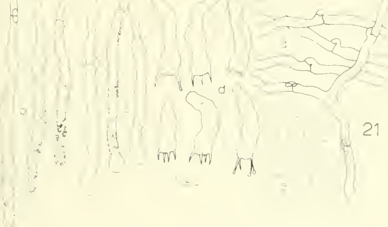


Fig. 21. *Poria apacheriensis* (JPL 407 and 409). a. subicular hyphae; b. cylindric cystidia; c. capitate cystidia; d. basidia; e. basidiospores.

pores circular to angular, 4-6 per mm; margin abrupt, fertile or narrowly sterile, blackening with age; subiculum less than 1 mm thick, cream colored to pale buff; tube layers stratified, single layers up to 1 mm thick; hyphal system dimitic; subicular generative hyphae (Fig. 22a) inconspicuous, thin walled, with clamp connections, 2-3 μm diam; subicular skeletal hyphae (Fig. 22b) hyaline, thick walled, aspetate, with rare branching, 3-5 μm diam; tramal hyphae similar; fusoid cystidioles (Fig. 22c) present, barely projecting, 11-18 x 5.5-7 μm; basidia (Fig. 22d), broadly clavate, four-sterigmate, 14-18 x 8-9 μm; basidiospores (Fig. 22e) cylindric, subfusiform, hyaline, smooth, negative in Melzer's reagent, 8-10 x 3-4 μm.

Poria ferox causes a brown cubical rot with conspicuous cream colored to pale buff mycelial felts in the shrinkage cracks.

Voucher specimens: RLG 10126, on alligator juniper, Parker Canyon, Huachuca Mts., Santa Cruz Co., AZ; RLG 10817 and 10822, on alligator juniper, Indian Creek, Animas Mts., Hidalgo County, NM; RLG 10127, on alligator juniper, Parker Canyon Lake, Cochise Co., AZ (ARIZ).

PORIA RIMOSA Murr., Mycologia 12: 91. 1920.

Basidiocarps perennial, sometimes developing as scattered patches on a cottony mycelial mat on the surface of the substratum, often becoming rimose with age; pore surface Light Ochraceous Buff to Cinnamon Buff, pores 5-7 per mm, angular; hyphal pegs present; dissepiments at first appearing tomentose under a 30X lens, thick, becoming thin and splitting with age; tube layer ivory to straw colored, up to 2 mm thick; context concolorous with tubes, soft, fibrous, up to 0.5 mm thick, taste mild; hyphal system dimitic; subicular generative hyphae (Fig. 23a) thin walled, with abundant clamp connections, often branched, 2-3 μm diam; subicular skeletal hyphae (Fig. 23b) thick walled, apparently nonseptate, 2-3 μm diam; tramal hyphae predominantly thin walled, with clamp connections, 2-3 μm diam; cystidia (Fig. 23c) scarce to common, not incrusted, thin walled, hyphoid, up to 2.5 μm diam and projecting up to 25 μm beyond the hymenium; basidia (Fig. 23d) clavate, four-sterigmate, 10-13 x 4-6 μm; basidiospores (Fig. 23e) hyaline, smooth, negative in Melzer's reagent, allantoid, 4-5.5 x 1-2 μm.

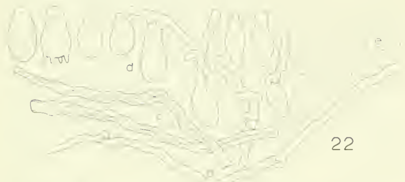
Poria rimosa causes a white heartrot of living trees and is also found on dead standing and fallen junipers. In the advanced stages the rot is characterized by small empty pockets. It has a wide distribution in western North America (Gilbertson, 1961).

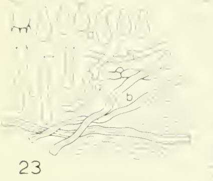
Voucher specimens: RLG 6961, on alligator juniper, Sponsellor Lake Rd., Navajo Co., AZ; RLG 6963, on one-seed juniper, between Show Low and Snowflake, Navajo Co., AZ; RLG 7560, on one-seed juniper, Stoneman Lake Rd., Coconino Co., AZ; K. D. Butler, on alligator juniper, Mingus Mt., Yavapai Co., AZ; JLL 9106, on one-seed juniper, Silver Creek, near Portal, Cochise Co., AZ; RLG 10603, on Utah juniper, Seegmuller Mt. area near Wolf Hole, Mohave Co., AZ (ARIZ).

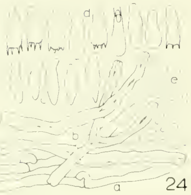
PORIA SINUOSA (Fr.) Cke., Grevillea 14: 113. 1886.

Polyporus sinuosus Fr., Syst. Myc. 1: 381. 1821.

Basidiocarps annual, often widely effused, tough, corky, easily separable, taste resinously bitter; margin fertile or narrowly sterile, Light Buff, soft, fimbriate, to 1 mm wide; pore surface Cream Color or drying to Cinnamon Buff, the tubes to 3 mm long, the pores circular to angular or sinuous, 2-4 per mm, with thick, entire dissepiments that become thin and deeply lacerate; subiculum whitish, corky, azonate, to 2 mm thick; hyphal system dimitic; subicular generative hyphae







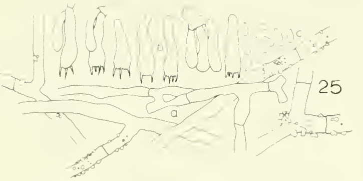


Fig. 22. *Poria ferox* (RLG 10817), a, subicular generative hyphae; b, subicular skeletal hyphae; c, fusoid cystidioles; d, basidia; e, basidiospores.

Fig. 23. *Poria rimosa* (RLG 6961 and 6963), a, subicular generative hyphae; b, subicular skeletal hyphae; c, hyphoid cystidia; d, basidia; e, basidiospores.

Fig. 24. *Poria sinuosa* (HHB 1133), a, subicular generative hyphae; b, subicular skeletal hyphae; c, fusoid cystidioles; d, basidia; e, basidiospores.

Fig. 25. *Poria tarda* (RLG 10135), a, subicular hyphae; b, basidia; c, basidiospores.

(Fig. 24a) thin walled, rarely branched, with clamp connections, 2-4 μm diam; subicular skeletal hyphae (Fig. 24b) thick walled, aseptate, rarely branched, 2-5 μm diam; fusoid cystidioles (Fig. 24c) 12-15 x 3-4 μm; basidia (Fig. 24d) clavate, four-sterigmate, with a basal clamp connection, 11-13 x 4.5-5 μm; basidiospores (Fig. 24e) cylindric, some slightly curved, hyaline, smooth, negative in Melzer's reagent, 4-6 x 1.5-2 μm.

Poria sinuosa causes a brown cubical rot of conifer logs and slash. It is distributed throughout western coniferous forests.

Voucher specimen: H. H. Burdsall 1133, on *Juniperus* sp., Valencia Co., Cibola Nat. Forest Rd. No. 3480 near Grants, NM (ARIZ).

PORIA TARDA (Berk.) Cke., Grevillea 14: 109. 1886.

Polyporus tardus Berk., London J. Bot. 4: 56. 1845.

Basidiocarps annual, usually adnate, pore surface rose pink to cream, usually drying Pinkish Buff to Light Buff; tubes originating as isolated cupules and then uniting; pores 3-5 per mm; sterile margin usually rather wide, thinning out; context white to cream, soft, thin, hyphal system monomitic; subicular hyphae (Fig. 25a) hyaline, thin walled, simple-septate, occasionally ampullate at the septa, frequently branched at right angles, some with crystalline incrustation, 2.5-6 μm diam; tramal hyphae similar; cystidia none; basidia (Fig. 25b) clavate, four-sterigmate, 15-20 x 4-5 μm; basidiospores (Fig. 25c) oblong to cylindric-ellipsoid, hyaline, smooth, negative in Melzer's reagent, 4-5 x 2-2.5 μm.

Poria tarda is a common fungus in southern Arizona and has been found on dead wood of many trees and large shrubs from the Sonoran Desert up to the ponderosa pine forest. It causes a white rot.

Voucher specimens: RLG 10135, on alligator juniper, Sunnyside, Huachuca Mts., Cochise Co., AZ; RLG 10197, on alligator juniper, Canelo Rd., Santa Cruz Co., AZ; ERC 71-118, on alligator juniper, Sunnyside, Huachuca Mts., AZ (ARIZ).

PYROFOMES DEMIDOFFII (Lév.) Kotl. et Pouz., Repert. nov. Spec. Regn. veg. 69: 140. 1964.

Polyporus demidoffii Lév. in Demidoff, Voy. Russ. Merid. 2: 92. 1842.

Basidiocarps perennial, sessile, solitary, ungulate, often becoming columnar, to 15 cm wide, 7 cm thick, and 10 cm high; upper surface brownish and tomentose in young specimens, becoming blackened and rimose with age, concentrically sulcate; margin rounded, Warm Buff to Ochraceous Buff, finely tomentose to blackened and rimose in older specimens; pore surface Light Ochraceous Buff to Ochraceous Buff, smooth, the pores rounded, 2-3 per mm; dissepiments thick, entire; context Orange Cinnamon to Cinnamon Rufous, woody, azonate; tube layers Ochraceous Buff to Antimony Yellow at first, eventually becoming filled with mycelium and concolorous with con-

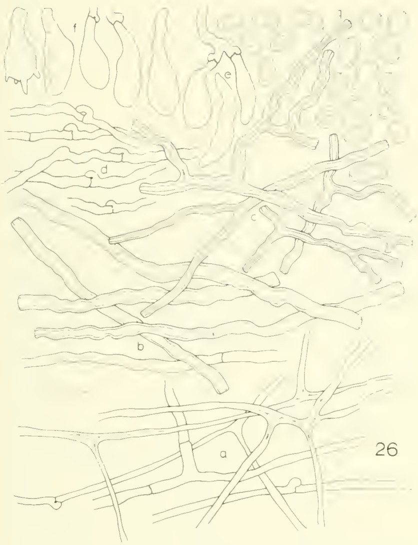


Fig. 26. *Pyrofomes demidoffii* (RLG 10600). a, hyphae from mycelial felts; b, contextual skeletal hyphae; c, much-branched skeletal hyphae from trama; d, contextual generative hyphae; e, fusoid cystidioles; f, basidia; g, basidiospores

text, indistinctly stratified, each layer to 7 mm thick; hyphal system dimitic; contextual generative hyphae (Fig. 26d) difficult to discern, thin walled, hyaline in KOH and Melzer's reagent, with clamp connections, 2.5-4 µm diam; contextual skeletal hyphae (Fig. 26b) moderately thick walled, rarely septate, with rare branching, pale brownish in KOH and dextrinoid in mass in Melzer's reagent, 3-5.5 µm diam; tramal tissue similar but with some much-branched skeletal hyphae (Fig. 26c), 2-5 µm diam; tramal tissue distinctly dextrinoid in Melzer's reagent; hyphae of mycelial felts (Fig. 26a) in wood frequently branched, some thick walled, aseptate, 1-3 µm diam, others thin walled, simple-septate or with occasional clamp connections, 1.5-3.5 µm diam; inconspicuous fusoid cystidioles (Fig. 26e) in hymenium, thin walled, not incrusted, 20-30 x 3-5 µm; basidia (Fig. 26f) broadly clavate from a narrow base, four-sterigmate, with a basal clamp connection, 22-35 x 8-10 µm; basidiospores (Fig. 26g) pale brownish, slightly dextrinoid in Melzer's reagent, ovoid to broadly ellipsoid or more elongated, angular, thick walled, most truncate at apex with an inconspicuous germ pore, 6-12 x 5-7 µm.

Pyrofomes demidoffii is probably the most important heartrot fungus in western junipers. It causes a white rot with abundant mycelial felts in the decayed wood. It has been referred to as *Fomes juniperinus* (von Schrenk) Sacc. et Syd. in most American literature.

Voucher specimens: RLG 6960, on one-seed juniper, between Show Low and Snowflake, Navajo Co., AZ; RLG 7384 and 7815, and ERC 71-28 and 71-326, on one-seed juniper, Sycamore Canyon, Atascosa Mts., Santa Cruz Co., AZ; RLG 7559, Stoneman Lake Rd., 7 mi E of Highway 79, Coconino Co., AZ; RLG 7562, on one-seed juniper, Dry Creek, 6 mi W of Sedona, Coconino Co., AZ; RLG 7890, on Utah juniper, South Rim, Grand Canyon Nat. Park Coconino Co., AZ; RLG 9875, on Utah juniper, Mt. Trumbull, Mohave Co., AZ; JLL 9070, on one-seed juniper, Silver Creek, Chiricahua Mts., Cochise Co., AZ (ARIZ).

PANUS FULVIDUS Bres., Fung. Trid. II, p. 56. 1900.

Basidiocarps centrally stipitate, single to gregarious; pileus circular, 0.5-3 cm diam; upper surface pale brownish (Cinnamon Buff to Clay Color) with radial fibrillar scales; stipe Light Buff at apex to Buffy Brown at the base, glabrous to minutely pubescent or scaly, to 3 mm diam and 2 cm long; gills pinkish cream to pale buff when dried, distant, free to adnate, edges sinuous and distinctly granulose under a 30X lens; contextual hyphae variable, some (Fig. 27a and b) simple-septate, with occasional branching, thin to slightly thick walled, 2.5-6 µm diam, others (Fig. 27c) very thick walled to almost solid, aseptate, rarely branched, 5-9 µm diam; pleurocystidia (Fig. 27d) fusoid, barely projecting, 35-60 x 6-8 µm; cheilocystidia similar; basidia (Fig. 27e) clavate, four-sterigmate, simple-septate at base, 38-60 x 9-13 µm; basidiospores (Fig. 27f) broadly cylindric, slightly curved, hyaline, smooth, negative in Melzer's reagent, 12-16 x 5.5-7 µm.

Panus fulvidus causes a brown cubical rot and is a common fungus on dead standing and fallen junipers and also on juniper fence posts in southern Arizona.

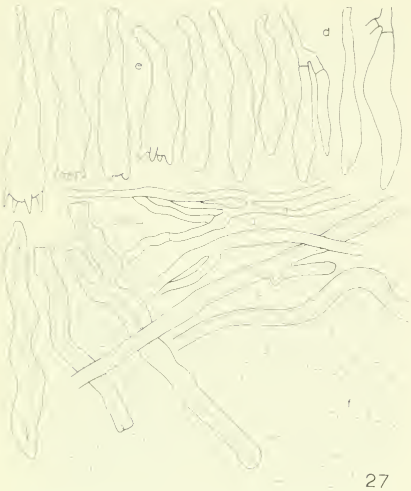


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Fig. 27. *Panus fulvidus* (ERC 71-132 and 71-158), a, thin-walled contextual hyphae; b. slightly thick-walled contextual hyphae; c. thick-walled to solid contextual hyphae; d. fusoid pleurocystidia; e. basidia; f. basidiospores.

Voucher specimens: ERC 71-132, on alligator juniper, Scotia Canyon, Huachuca Mts., Cochise Co., AZ; RLG 10044, on juniper fence post, Washington Camp, Patagonia Mts., Santa Cruz Co., AZ; RLG 10258, on juniper fence post, Sycamore Canyon, Atascosa Mts., Santa Cruz Co., AZ (ARIZ).

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BODY SIZE, ORGAN SIZE, AND SEX RATIOS IN ADULT AND YEARLING BELDING GROUND SQUIRRELS

Martin L. Morton[1] and Robert J. Parmer[2]

Abstract.— A five-year study of Belding ground squirrels was conducted at high altitude in the Sierra Nevada. Body weight and body length varied seasonally depending upon the fat depletion-deposition cycle, age, and sex. Adult males tended to be heavier and longer than adult females, particularly in the last half of the active season. A similar pattern was present in yearlings. Yearling squirrels were often distinguishable from adults on the basis of body size. Mean body weights were greater in adults throughout the season, and mean body lengths were greater in adults through the first half of the season. Adults also had larger internal organs than yearlings at the beginning of the season. In liver and heart this difference was sustained. Sex ratios in adults and in yearlings were 1:1 but there was considerable spatial and temporal asymmetry in distribution of the sexes. Males tended to live in areas peripheral to lush meadows occupied by females and young.

The Belding ground squirrel (*Spermophilus beldingi beldingi*) is a hibernator that lives in the central Sierra Nevada Mountains mainly from the eastern divide to the edge of the Great Basin at altitudes between 1,825 m and 3,650 m (Storer and Usinger, 1970). During a five-year, mark-release study of *S. b. beldingi* our records of retrapped animals enabled us to compile data on individuals of known age and sex for prolonged periods. In the course of this study it became clear that three functional groups, based upon age, existed within the population: juveniles, yearlings, and adults. Characteristics of juveniles have been previously reported (Morton, Maxwell, and Wade, 1974). Herein we report on seasonal changes in body size, organs, and on sex ratios in both yearling and adult *S. b. beldingi*.

Methods

The study was conducted from 1969 through 1973 in meadows and their bordering areas in Lee Vining Canyon, Mono County, California. Most of our information stems from work done at Big Bend (elevation ca 2,100 m) and especially at Tioga Pass (elevation ca 3,000 m). The active seasons are similar in duration for populations at both areas but may begin six weeks or more apart due to climatic differences associated with altitude (Morton, 1975). All data reported on body weights, body lengths, and sex ratios of squirrels of known age are from Tioga Pass animals. Data on organ weights were combined for the two populations at 10-day intervals throughout the active season in order to bolster sample size.

Squirrels were captured alive in Tomahawk wire-mesh traps baited with peanut butter. Those to be released were toe-clipped, and those retained for specimens were etherized. In some cases specimens were collected with a .22 caliber rifle. Body weights were measured to the nearest 0.1 g on a pan balance. Body lengths were taken with calipers to the nearest 0.1 cm. Wet weights of freshly excised and debrided organs were measured to the nearest 0.01 g on an analytical pan balance.

Certain small meadows or sections of large meadows were used only for mark-release studies. Separate data logs were maintained for each toe-clipped animal. In our terminology juveniles are the young of the year, yearlings were born in the preceding year, and adults are all animals older than yearlings.

Results

The first *S. b. beldingi* to emerge each season were adult males. Within a few days, however, some adult females and yearlings could be found. The pace of emergence varied somewhat from year to year, depending upon snow cover. Adults tended to enter hibernation earlier than yearlings. On the average each individual was active above ground for about three months (Morton, 1975).

Body weight.— There were large seasonal differences in body weight due primarily to fat depletion or deposition and to sex and age differences (Fig. 1).

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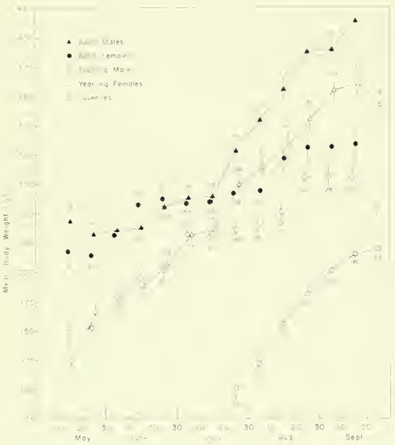

Fig. 1. Seasonal change in mean body weight of *Spermophilus beldingi beldingi* at Tioga Pass. Data were accumulated over five seasons, 1969-73. Numerals indicate sample size; vertical bars denote ± 2 S.E.

Upon emerging in mid-May adult females at Tioga Pass were lighter than adult males, but during pregnancy they became heavier than males. In late July and for the remainder of the active season mean weights of adult males were significantly greater than those of adult females ($P<0.05$). The sexes of yearlings were not different in weight until late July. Thereafter, as in adults, males were heavier. Seasonal trends in body weight were much the same for each sex, particularly in the second half of the season. During the first half of the season yearlings were still growing rapidly. As a group, yearlings never achieved adult weight. Adults were significantly heavier ($P<0.05$) than their yearling counterparts of the same sex at every class interval throughout the season. The large weight gain observed in all animals during the last half of the season was due to fat deposition (Morton, 1975).

Body length.— Growth in yearlings, as indicated by body length, occurred throughout the season (Fig. 2), but from

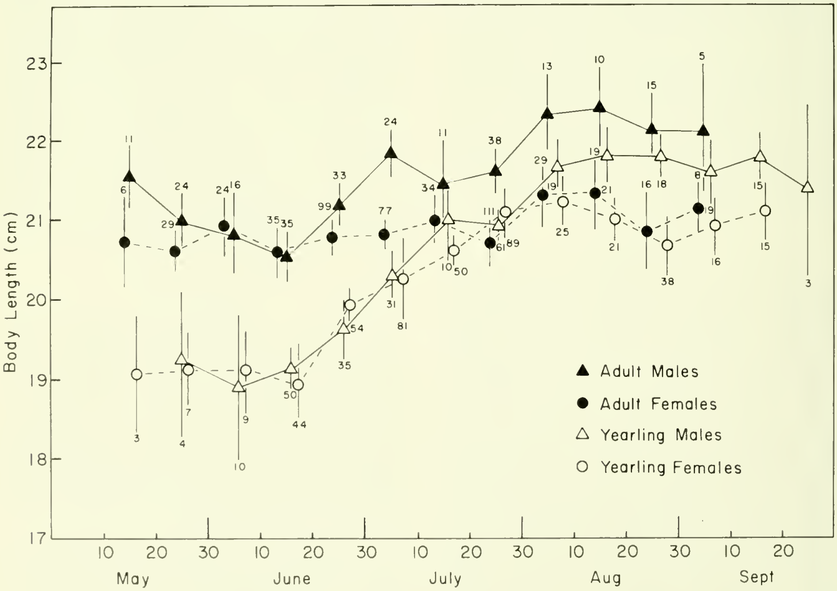

Fig. 2. Seasonal change in mean body length of *Spermophilus beldingi beldingi* at Tioga Pass. Data were accumulated over five seasons, 1969-73. Numerals indicate sample size; vertical bars denote ± 2 S.E.

mid-July on yearling females as a group were indistinguishable from adult females in body length. The same was true of males except that the smaller males handled in August and September invariably were yearlings.

Body length increased in adult males as the season progressed, suggesting that maximum size in *S. b. beldingi* males may not be reached until beyond their second year of life.

Organ weights.— Liver weights increased rapidly following emergence in all animals (Fig. 3), but the increase was more rapid in females than in males. Between the third and sixth weeks of activity livers of females were larger than those of males ($P<0.05$). Liver hypertrophy in females was coincident with lactation.

By the twelfth week of the season yearlings had livers of adult size. Livers for all ages and sexes were smaller at the end of hibernation than at the beginning. Apparently this organ atrophied during hibernation.

The heart, kidneys, and spleen, were larger in adults than in yearlings during the first part of the season (Fig. 4). This difference was particularly noticeable and prolonged in heart weight.

Sex Ratios.— During the five years of this study a total of 341 yearlings (170 males and 171 females) and 484 adults (238 males and 246 females) were handled. The sex ratio for either age group did not differ from 1:1 according to a chi-square test ($P>0.50$).

Discussion

Body size.— Although yearling ground squirrels often represent a substantial por-

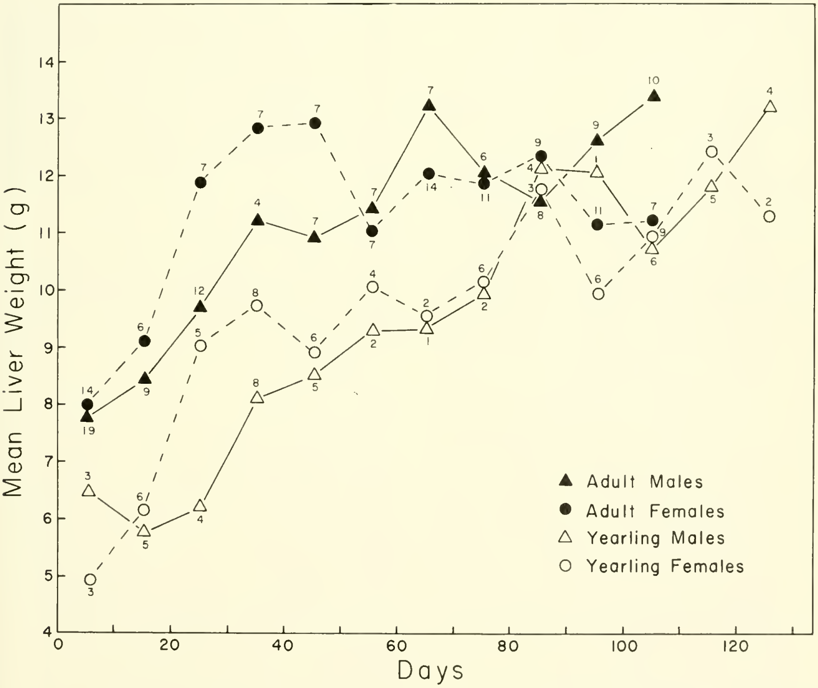

Fig. 3. Seasonal changes in mean liver weight of *Spermophilus beldingi beldingi* from Big Bend and Tioga Pass. Numerals indicate sample size. Day 0 of abscissa refers to time first squirrels emerged from hibernation.

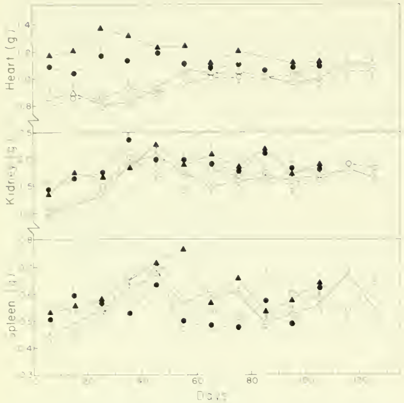

Fig. 4. Seasonal changes in mean weight of spleen, kidneys, and heart in *Spermophilus beldingi beldingi* from Big Bend and Tioga Pass. Numerals indicate sample size. Symbols as in Figure 3. Day 0 of abscissa refers to time first squirrels emerged from hibernation.

tion of the population and may interact in unique ways with other members (Michener and Michener, 1973), there is little published evidence that they differ externally from older animals. Even in such large-bodied species as *S. undulatus* juveniles reach adult size, or nearly so, by the time they are ready for hibernation (Mayer and Roche, 1954). *A priori* this might be predicted since captive juveniles of hibernatory *Spermophilus*, particularly those from high latitude or high altitude, tend to be precocious and to have exceptionally high growth rates (Clark, 1970; Morton and Tung, 1971). In the case of *S. b. beldingi*, at least, by the time they enter hibernation feral juveniles have foot and tail lengths indistinguishable from those of adults (Morton and Tung, 1971). Nonetheless, neither maximum body weight nor maximum body length is achieved in *S. b. beldingi* until well into the second or possibly even third year of life. Furthermore, we have found that yearling males are sexually immature and do not reproduce (Morton and Gallup, unpubl.). Yearling females do reproduce. Similar age differences in reproductive capacity have been found in *S. armatus* (Slade and Balph, 1974).

The differences in body size noted in age classes of *S. b. beldingi* probably are not unique among ground squirrels. Such differences are likely to be overlooked unless the investigator examines large numbers of animals of known age over a span of several consecutive seasons.

Sex ratios.— An unbalanced sex ratio in favor of females has been reported for many ground squirrel populations. This ratio may approach or exceed 3:1 (McCarley, 1966; Michener and Michener, 1971; Sheppard, 1972; Turner, 1972). In a few cases, however, the ratio found did not differ significantly from 1:1 (Clark, 1970; Murie, 1973; present study). In his study of *S. b. oregonus*, Turner (1972) found that the sex ratio was 1:1 in juveniles. He suggests that because juvenile males tend to wander and explore more than females they incur greater mortality, resulting in an unbalanced sex ratio in older animals. In *S. b. beldingi* the sex ratio in juveniles is also 1:1; males probably wander more than females in that they have larger home ranges than females and are more likely to expand their range late in the season (Morton, Maxwell, and Wade, 1974). Although this behavior would seem to make juvenile males more susceptible to predation, we have no evidence that it does. To the contrary, males and females occur in equal numbers in both yearlings and adults. The sexes are not distributed randomly throughout the habitat occupied, however. In our trapping at burrow systems located in lush meadow areas reserved for mark-release studies, adult females outnumbered males by 1.3:1 when all data were summed. The ratio tended to fluctuate seasonally, however, and was sometimes near 3:1, particularly at midseason. We often captured adult males at a particular burrow system only a few times per season, during the first days or weeks following emergence and again at the very end of the season. This suggests that some males were forced from the colony by conflicts associated with reproduction and were able to return only in time to enter their traditional hibernaculum. If this is correct, it follows that displaced males should be found in areas peripheral to main colonies. We found this to be the case. When males were desired for specimens, they could usually be found by collecting animals scattered in lodgepole pine stands fringing meadows, and in rocky outcrops and talus slopes in steep areas above the meadows

A tendency for males to live in areas peripheral to the main colonies has been observed previously in *S. armatus* (Balph and Stokes, 1963) and in *S. richardsonii* (Quanstrom, 1971). Turner (1972) did not believe, however, that this occurred in *S. b. oregonus*. The spatial distribution of the sexes could vary enormously depending upon such factors as habitat physiography and upon intrinsic characteristics of the population itself.

Undoubtedly unbalanced sex ratios exist in many ground squirrel populations. Such ratios may be a function of interpopulational or interspecific differences in breeding systems and social organization (Murie, 1973). However, an investigator who confines his work to locations with maximum animal density or to those of easy accessibility could obtain an inaccurate measurement of sex ratio.

ACKNOWLEDGMENTS.— We wish to thank John Gallup, Roland Leong, Catherine Maxwell, Allan Tway, and Charles Wade for assistance in trapping operations. Southern California Edison Co. provided housing for two seasons. Financial support was provided by Occidental College and by National Science Foundation Grant GB 29146X1.

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PHOTOPERIODIC RESPONSES OF PHENOLOGICALLY ABERRANT POPULATIONS OF PIERID BUTTERFLIES (LEPIDOPTERA)

Arthur M. Shapiro[1]

Abstract.— Two local pierid populations in western North America showing regionally aberrant phenologies were investigated in the laboratory. Neither a partially bivoltine *Pieris napi* from the Sierra Nevada foothills in El Dorado County, California (surrounded by univoltine populations), nor a vernal-univoltine *P. occidentalis* from a foothill outlier of the Colorado Front Range (below bivoltine populations) showed unusual responses to controlled developmental regimes in the laboratory. Their unusual phenologies are hypothesized to be the product of microclimate. Failure to undergo genetic adaptation to unusual microclimates is discussed with particular reference to the presence or absence of gene flow from nearby normal populations.

The timing of life-history phenomena in an insect population is determined by physiological responses to environmental stimuli. These proximate controls reflect a genetic basis believed to be the product of natural selection for seasonal cycles appropriate to the environment of the population. In the western United States topography has a dramatic impact on climate, and great differences may occur over short ground distances. How closely can insect populations adapt to their immediate climates on a microgeographic scale? Phenological adaptation is merely one case of the more general problem of population differentiation (cf. Ehrlich and Raven, 1969; Ehrlich et al., 1975). In most organisms, at least prior to the advent of electrophoretic genetics, population differentiation was assessed on the basis of visible phenotypic characters. Such characters, like the enzyme systems studied by electrophoresis, are often not translatable into specific selection pressures. In markedly seasonal climates the nature of selective pressures acting on phenology may be very apparent. Where local deviations from the broad geographic pattern of voltinism are observed in a species, the potential exists for the demonstration of microgeographic (or ecotypic) differentiation. This is the fourth paper in a series exploring the evolution of seasonality in the butterfly genus *Pieris* in western North America.

In various multivoltine Pieridae both phenotype and diapause are under photoperiodic control. The two sets of developmental options (diapause/direct development; vernal/estival phenotype) may be physiologically coupled (*Pieris napi* Linnaeus complex) or not (*P. protodice* Boisduval & LeConte, *P. occidentalis* Reakirt). Recent studies have shown that univoltinism in both groups is derivative from multivoltinism, accompanying invasion of a short-summer climate (*P. occidentalis*, Shapiro, 1975a) or persistence in a progressively drier one (*P. napi*, Shapiro, 1975b). Such patterns are defined over broad geographic areas. California *P. napi*, for example, is differentiated into a commonly bivoltine, heavily pigmented subspecies in the coastal summer-fog belt and a univoltine, more lightly marked subspecies in the interior, where summers are clear and hot. The transition between the subspecies appears to be in the form of a steep cline through the central Coast Ranges (Shapiro, in preparation).

Recently Lees and Archer (1974) have reported the existence of phenological differences among *napi* populations on a much finer scale. They have found apparently relict univoltine populations in suitable (bog-heath) habitats completely surrounded by multivoltine ones in the British Isles. Their preliminary interpretation of this situation is that it provides evidence for multiple invasions of Britain by *napi* stocks having different phenological characteristics and source regions. In the course of recent work on pierid phenology and evolution, the existence of regionally aberrant populations has been brought to my attention in both the *napi* and *protodice-occidentalis* groups. In both cases the populations appear to be unique, rather than forming a repeating pattern as in British *P. napi*. They would therefore seem to be good candidates for local genetic differentiation under atypical microclimates.

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Pieris napi in the Sierra Foothills

Pieris napi from interior California are, as noted above, univoltine and monophenic in nature. Under laboratory conditions they can be reared without diapause; then they produce the estival phenotype "*castoria*" virtually unknown in the wild in the interior (Shapiro, 1975b). In June 1974 Mr. William Patterson of Sacramento, California, took several wild "*castoria*" of both sexes in the canyon of the American River below Auburn in the Sierra Nevada foothills (El Dorado County, 650 feet). The occurrence of a second brood there was confirmed in 1975. *P. napi* is common in the canyon, producing its usual vernal phenotype in March. The second brood, which is much scarcer, unlike the first is extremely localized within the canyon—at present being known from only two densely shaded ravines where the introduced cruciferous weed watercress (*Nasturtium officinale* R. Br. = *Rorippa nasturtium-aquaticum* Schinz. & Thell.) grows in permanent streams (Fig. 1). Most of the wild June butterflies are identical to laboratory-bred Sierran "*castoria*" (Fig. 2).

On 29 March 1975 nine male and three female first-brood, vernal phenotype *napi* were collected in one of these ravines. These included two copulating pairs in which the females were soft-winged, indicating that they had developed in the ravine itself. The eggs from these females were used in photoperiod experiments (Table 1). (Rearing methods are described in Shapiro, 1975a and 1975b.) The results are entirely typical for Sierran stock and do not suggest that American River material has a greater propensity to develop directly than do stocks from purely univoltine localities, at least under our laboratory regimes. However, this is not particularly surprising. The second brood of *napi* in the American River gorge is much rarer than the first, indicating that is is only partial; its numbers also fluctuate from year to year.

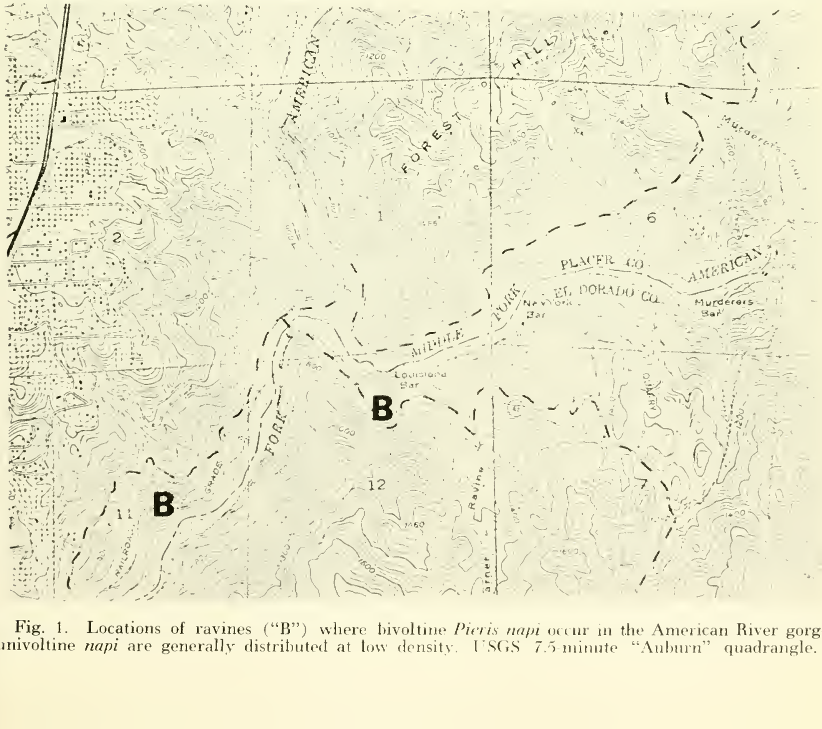

Fig. 1. Locations of ravines ("B") where bivoltine *Pieris napi* occur in the American River gorge; univoltine *napi* are generally distributed at low density. USGS 7.5-minute "Auburn" quadrangle.

TABLE 1. Incidence of diapause (D) and nondiapause (ND) pupae in bivoltine (American River, 650') and univoltine (Placerville, 1800') *Pieris napi* from El Dorado Co., Calironia, reared on watercress at 27 C under two photoperiods.

Photophase:	Continuous		15 hr	
Stock: Pupae:	D	ND	D	ND
American River	15	29	16	6
Placerville	10	23	18	7

(In 1975 three trips by Patterson and Shapiro in season turned up only two males and one female. A later search of the host plant at the optimum time failed to turn up any *napi* immatures, although ten *Pieris rapae* larvae were found.) These circumstances suggest that the production of a second brood here is accidental, resulting from the peculiarly cool and moist conditions within the ravines. There is no evidence that the bivoltine sites are in any sense isolated from adjacent univoltine ones, nor is it clear that there is successful reproduction by the second brood in all years nor even that there is genetic continuity from year to year in the ravines; perhaps a few pu-

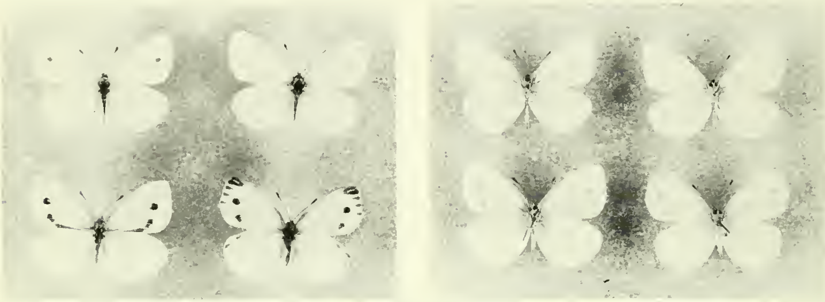

Fig. 2. Wild second-brood *Pieris napi* from the American River gorge, collected by W. Patterson in June 1974 (males at top; dorsal (left) and ventral (right) surfaces). The heavily marked female is atypical for an inland population.

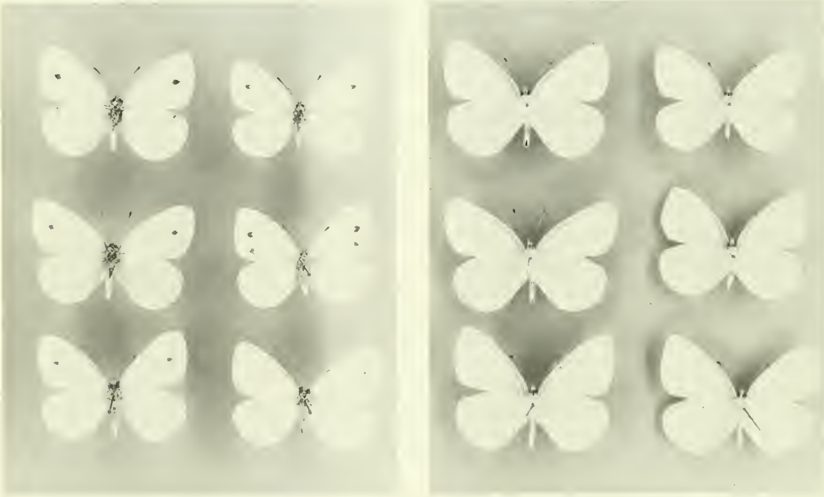

Fig. 3. Phenotypes of representative lab-reared nondiapause *Pieris napi* from the American River stock: 27 C, continuous light: dorsal (left) and ventral (right).

pae will develop directly there whenever any female *napi* happens to colonize them. Experienced California collectors (R. L. Langston, B. Walsh) agree that even near the coast some localities produce second-brood *napi* every year and others only rarely or sporadically. Experiments have shown both developmental and phenotypic differences between coastal and inland stocks but not among the coastal stocks themselves.

Watercress is known to be host of *P. napi* in various Sierran sites up to about 5,000 feet (Shapiro, 1975c). The only other record of a Sierran "*castoria*" known to me is a fresh male taken flying among first-brood vernal *napi* at Lang Crossing, Nevada County, 4,500 feet, 9 June 1975. At this locality *napi* feeds on both watercress and native vernal crucifers. There are several possible explanations of this odd individual, but to test the hypothesis that watercress feeding itself inhibits diapause, split-brood experiments were conducted in 1975 using an Inner Coast Range stock (Gates Canyon) with no previous exposure to the plant. No evidence of a dietary influence on the incidence of diapause was found in this univoltine strain (Table 2).

TABLE 2. Incidence of diapause (D) and non-diapause (ND) pupae in two split broods of a *Barbarea verna*-feeding univoltine *Pieris napi* (Gates Canyon, Inner Coast Ranges, Solano Co., 750') reared at 27 C on continuous light. None of the differences was significant.

Brood	Host	Pupae: D	ND	Mean ND developmental time in days
1	*Brassica kaber*[a]	7	21	25.2
	Nasturtium officinale[b]	5	11	25.3
3	*Brassica kaber*[a]	6	14	25.6
	Lepidium latifolium[b,c]	5	16	24.6

Notes: (a) Tops. (b) Elongating rosettes. (c) In subsequent experiments mature tops did not support development. Butterflies in this brood were stunted.

Pieris occidentalis in Colorado

Haystack Mountain (5,589 feet) is an isolated hill eight miles northeast of Boulder, Boulder County, Colorado (Fig. 4), where Dr. Ray E. Stanford of Denver has for several years taken small, dark vernal "*calyce*" phenotypes of *Pieris occidentalis* indistinguishable from the single brood above treeline in midsummer (Fig. 5). He has no summer records of *P. occidentalis* from Haystack Mountain but finds its lowland sibling *P. protodice* there in summer instead. Because *P. protodice* winters only very locally but colonizes widely in summer, this is not surprising; it does however, raise the possibility that *P. occidentalis* has undergone a phenological shift to univoltinism in

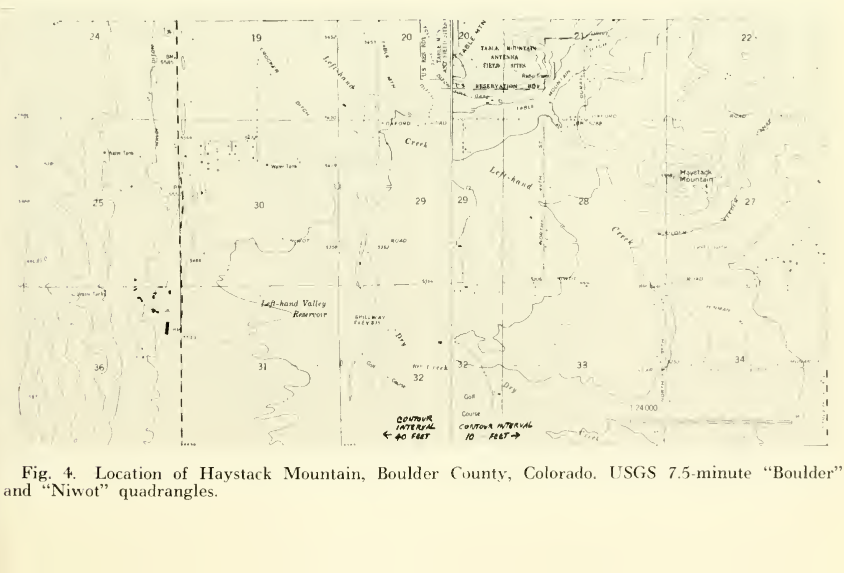

Fig. 4. Location of Haystack Mountain, Boulder County, Colorado. USGS 7.5-minute "Boulder" and "Niwot" quadrangles.

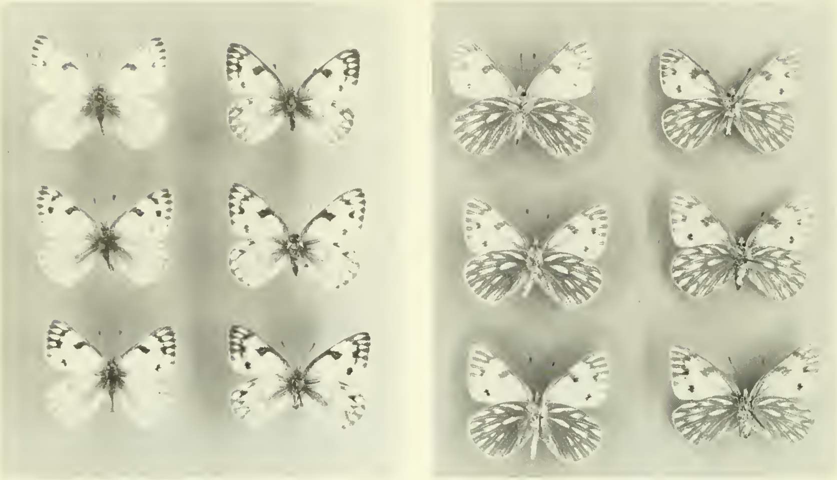

Fig. 5. Wild *Pieris occidentalis*, vernal phenotype ("*calyce*"), from Haystack Mountain, collected by R. E. Stanford. Males at left; dorsal (left) and ventral (right) surfaces.

response to competition from *P. protodice* (although no such phenomenon is known at other localities where the two are sympatric). Haystack Mountain is probably the lowest elevational record for *P. occidentalis* in Colorado. In the Rockies proper it is bivoltine at middle elevations (perhaps locally trivoltine) and univoltine in the Alpine zone (cf. Brown, Eff, and Rotger, 1957) and has two seasonal phenotypes (Shapiro, 1975d).

A laboratory stock was established from ova laid by five females collected by Stanford on 6 April 1975. Under laboratory conditions their developmental and phenotypic responses (Table 3 and Fig. 6) were identical to both Sierran multivoltine and Colorado Alpine stocks (Shapiro 1974, 1975d). Once again we have no experimental evidence for the evolution of a phenological ecotype and are therefore forced to look for microclimatic explanations. Since Haystack Mountain is effectively in the Great Plains climatic regime, which is hotter and drier than the usual regime of *P. occidentalis*, it may not be surprising that conditions there would be associated with summer dormancy. This question can be settled only by laboratory duplication of Haystack Mountain conditions or by testing the developmental responses of multivoltine *P. occidentalis* stock from elsewhere reared at Haystack Mountain. We hope to carry out such experiments within the next couple of seasons.

Phenological differences are known between plains and lower montane populations of a number of Colorado butterflies (J.A. Scott, R.E. Stanford, pers. comm.), but they may go in a direction opposite to those observed in *Pieris occidentalis*. Two species (*Colias alexandra* Edwards, Pieridae; *Plebeius icarioides* complex, Lycaenidae, both Legume feeders) are bivoltine on the plains and univoltine in the mountains. The basis for these differences is uninvestigated.

With no evidence for genetic differentiation of Haystack Mountain *occidentalis*, the attractive hypothesis of competitive

TABLE 3. Incidence of diapause (D) and nondiapause (ND) pupae in vernal-univoltine (Haystack Mountain, Colordao, 5,589') and bivoltine (Donner Pass, Colorado, 7,000') *Pieris occidentalis* reared on *Brassica kaber* at 27 C.

Stock:	Photophase:	Continuous		15 hr	
	Pupae:	D	ND	D	ND
Haystack Mountain, 1975		0	22	0	9
Donner Pass, 1973		0	16	2	18

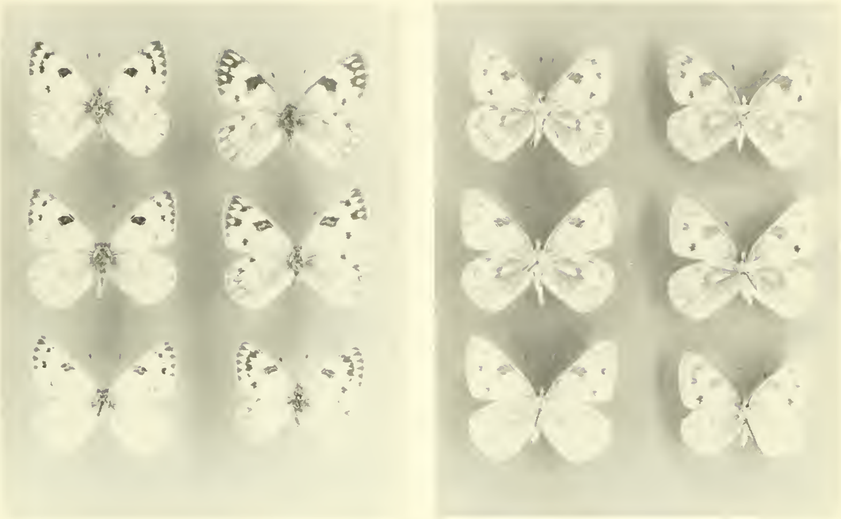

Fig. 6. Phenotypes of representatives lab-reared nondiapause *Pieris occidentalis* from the Haystack Mountain stock; 27 C. continuous light. Estival phenotypes characteristic of mutlivoltine. Males at left; dorsal (left) and ventral (right) surfaces.

seasonal displacement with *protodice* must be set aside. The host plants of both species on Haystack Mountain are unidentified. Both prefer species of peppergrass, *Lepidium*, throughout their ranges. On the plains most crucifers are vernal species, as in lowland California.

Discussion

Many instances are on record of ecotypic differentiation on a microgeographic scale, particularly in plants, which have more versatility in developing isolating mechanisms than do animals (Jain and Bradshaw, 1966).

As noted above, the lack of a genetic basis for biovoltinism in Sierran *Pieris napi* is not very surprising, granted the extremely restricted habitat and the extensive distribution of univoltine butterflies, with ample opportunity for gene flow. The failure of the Haystack Mountain *P. occidentalis* to differentiate is more intriguing. It is, of course, possible that it has differentiated and that the lab rearing regimes were too crude or inappropriately selected to show it. It is certain that experiments to date, involving simple manipulation of constant rearing temperatures and unchanging daylengths, have given an oversimplified picture of the developmental versatility of pierids in the field. If microclimate determines aberrant voltinism in these stocks, it is very likely that humidity, for example, may interact with photoperiod and temperature in controlling development in natural populations. The same genetic information may allow *Pieris occidentalis* to respond appropriately to regimes as diverse as those at Haystack Mountain (5,589 feet) and Loveland Pass (12,400 feet).

Given such plasticity, we may wonder whether the Baldwin effect (Simpson, 1953) might not come into play in populations in extreme environments. Briefly, the Baldwin effect postulates the buildup by selection of a genetically obligate basis for the adaptations produced via developmental plasticity. In an atypical *but predictable* climate like Haystack Mountain, might not the developmental flexibility characteristic of montane populations be lost? (Alaskan *Pieris occidentalis nelsoni* seem to be evolving in this direction: Shapiro, 1975a.) One important countervailing force would be gene flow, which is almost certainly operating on high-elevation univoltine *occidentalis* in Colorado (Shapiro, 1975d). Haystack Mountain is about 30 air miles from timberline and much closer than that to the montane zone, but how isolated it actually *is* is quite unknown. Nor is there any information bearing on how long *occidentalis* has been there—whether it is a Pleistocene relict or a recent colonization. There are much more isolated, certainly relict *occidentalis* populations in other localities east of the Front Range—the Black Hills of South Dakota and perhaps the Pine Ridge of northwestern Nebraska—which deserve study in this regard.

Acknowledgments

Of the collectors who provided vital information and who have been credited in the text, special thanks are due Mr. William Patterson and Dr. Ray Stanford, without whose help these experiments would have been impossible. Mr. Mark Kauzer assisted in field work and Mrs. Adrienne R. Shapiro in rearing. This research is part of a larger study of colonizing ability and the evolution of seasonality in *Pieris* funded by the Committee on Research, UCD, under grant D-804.

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ADDITIONAL RECORDS OF REPTILES FROM JALISCO, MEXICO

Philip A. Medica[1], Rudolf G. Arndt[2], and James R. Dixon[3]

Abstract. — Noteworthy records of reptiles from the state of Jalisco, Mexico, are presented. The first state records of *Coleonyx elegans nemoralis*, the second state record for *Geophis tarascae*, and notes on the distribution and reproduction of *Eumeces brevirostris indubitus* are discussed.

A small collection of amphibians and reptiles from Jalisco, Mexico, yielded several noteworthy specimens.

Coleonyx elegans nemoralis Klauber. One male (88 mm snout to vent length, SV) from 28.1 km SW Autlan, Jalisco, (Texas Cooperative Wildlife Collection, Texas A & M University, TCWC 48035), collected on 19 May 1974, elevation 518 m. There are three known specimens from Jalisco. The first, a male (Los Angeles County Museum, LACM 37568) 83 mm SV, from 74.2 km SW Autlan, Jalisco, was collected by J. R. Dixon and R. Heyer on 23 July 1967. This specimen has 10 preanal pores; 7-7 supralabials; 6-7 infralabials; 9 scales nostril to nostril; 6 gulars contacting mental; 4/4 gulars contacting first infralabials; 21 rows of tubercles across at midbody, and 16 fourth toe lamellae. Our specimen (TCWC 48035) has 11 preanal pores; 8-8 supralabials; 7-8 infralabials; 9 scales nostril to nostril; 5 gulars contacting mental; 4/5 gulars contacting first infralabials; 20 rows of tubercles across at midbody, and 17 fourth toe lamellae. The third specimen (Brigham Young University, BYU 41299), a male 85 mm SV, from 14.5 km N Barra de Navidad, Jalisco, was collected by J. Ottley on 30 October 1974. This specimen has 10 preanal pores; 6-7 supralabials; 7-8 infralabials; 9 scales nostril to nostril; 6 gulars contacting mental; 2/2 gulars contacting first infralabials; 21 rows of tubercles across at midbody, and 16 fourth toe lamellae. All specimens are within the range of variation described by Klauber (1945). These specimens extend the known range of this species inland some 107 km N from the coastal area of Colima, the heretofore northernmost portion of its known range (Klauber, 1945; Kluge, 1975).

Eumeces brevirostris indubitus Taylor. A series of 20 specimens, including 9 juveniles (24-30 mm SV, $\bar{x}$ = 26.7 mm) and 11 adults (52-75 mm SV, $\bar{x}$ = 61.2 mm), collected 25 km SE Autlan, Jalisco (TCWC 48036-48055), on 17 May 1974. This site is approximately 50 km W of the nearest reported locality and about 100 km SSE of the northernmost locality for this subspecies, both in Jalisco, thus partially filling the hiatus in the distribution described by Dixon (1969). Our specimens exhibit a significantly lower number of fourth toe lamellae (11-14, $\bar{x}$ = 11.8 ± 0.25) and superciliaries (5-6 to 7-7, $\bar{x}$ = 6.27 ± 0.08), but otherwise they fall well within the range of variation for *indubitus* given by Dixon (1969). This species is ovoviviparous according to Tanner (1958), who reported a female that contained two fully developed embryos. We secured one large female (75 mm SV, weight 6.67 g) that bore six live young between the time of capture and the next morning. Their range in length was 24-28 mm SV ($\bar{x}$ = 26.3 mm) and in weight from 0.37-0.46 g ($\bar{x}$ = 0.41 g). All *Eumeces* were found in pine-oak woodland under rocks within 20 m of a permanent stream, elevation 1,433 m. It is of interest to note that in this area there had been no appreciable rainfall since October 1973, and most decidous vegetation was devoid of leaves. Despite the apparent lack of moisture, *Eumeces b. indubitus* was capable of reproducing, perhaps owing to its ovoviviparous nature.

Geophis tarascae Hartweg. One female from 25 km SE Autlan, Jalisco (TCWC 47948), collected on 17 May 1974, elevation 1,433 m. This apparently is but the fifth known specimen of this species and the second from the state of Jalisco. Downs (1967) reported on three specimens from the type locality at Uruapan, Michoacan; Dixon (1968) reported one specimen from Nevado de Colima some 48 km to the E. Our specimen has 15 scale rows; 146 ventrals; 41 caudals; 0+1 temporals; 6 supralabials; 6 infralabials; 1 loreal; 1 postocular; no preocular, and 10/10 maxillary teeth. The first pair of chin shields is twice the length of the second pair; supraocular distinct, larger than loreal; internasals divided and distinct. The dorsum and tail are dark gray with blackish crossbands (40 on the body, 13 on tail) which do not extend across the venter; anterior crossbands 2-3 scale rows wide and bordered on the anterior and posterior by white-edged scales, posterior crossbands 1 scale row wide and highly irregular, frequently broken laterally and dorsally; head distinct from neck; color of rostral and prenasals similar to adjacent scales; eye twice into snout length; venter greenish white in life, heavily spotted with black. The total length is 236 mm, and the tail is 45 mm. This specimen has fewer ventrals than reported by Downs (1967) and Dixon (1968). Habitat was as described for *Eumeces brevirostris indubitus* above.

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The authors are indebted to Dr. Antonio Landazuri Ortiz, Director General de Fauna Silvestre of Mexico, for providing the necessary collecting permits. We also thank Drs. Wilmer W. Tanner and John W. Wright for loan of specimens in their care, and are grateful to Philip J. Medica for his untiring assistance in the field.

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INVASION OF BIG SAGEBRUSH (*ARTEMISIA TRIDENTATA*) BY WHITE FIR (*ABIES CONCOLOR*) ON THE SOUTHEASTERN SLOPES OF THE WARNER MOUNTAINS, CALIFORNIA

Thomas R. Vale[1]

Abstract.- White fir (*Abies concolor*) appears to be invading vegetation dominated by big sagebrush (*Artemisia tridentata*) on the southeastern slopes of the Warner Mountains of extreme northeastern California. The time of initial tree establishment within the shrubs was determined by increment borings. Possible causes of the invasion involving specific climatic conditions, fire history, and grazing use of the area during years of the establishment were explored. Heavy grazing by domestic livestock, particularly sheep, appears responsible for altering the sagebrush-grass vegetation and allowing tree invasion.

The Warner Mountains of extreme northeastern California rise to 3,000 m above sea level and support a forest dominated by white fir (*Abies concolor*) and ponderosa pine (*Pinus ponderosa*) (Fig. 1). The adjacent valleys lie at 1,220 m and, where not irrigated for pasture or hay crops, are covered by thick stands of big sagebrush (*Artemisia tridentata*) with an understory of herbaceous plants. In the southeastern portion of the range, the transition zone between coniferous forest and shrubs is characterized by populations of small fir trees within the brush, suggesting a recent downslope movement of the trees (Fig. 2). The cause of this invasion of sagebrush by white fir in the Warner Mountains is the focus of this paper.

Relation to Other Studies

Many observers have noted invasions of sagebrush by tree species in various parts of the Intermountain West. Although pinyon pines (*Pinus monophylla* and *P. edulis*) and junipers (*Juniperus* spp.) are the most common invaders of sagebrush (Arnold et al., 1964; Blackburn and Tueller, 1970; Burkhardt and Tisdale, 1969; Cottam and Stewart, 1940; Wright and Fisser, 1968), lodgepole pine (*Pinus contorta*) also has been found expanding into stands of *Artemisia* (Patten, 1969). Moreover, young trees of ponderosa pine in eastern Oregon and Jeffrey pine (*Pinus jeffreyi*) in eastern California may be readily observed within sagebrush areas along forest edges. Although all the above vegetation changes imply a recent establishment of trees in environments formerly unsuited to them, studies have not yet documented the invasion of the relatively xeric big sagebrush by so mesic a species as white fir.

In these previous studies, the initiation of tree establishment is often found to correlate with periods of intense livestock grazing. Cattle may deplete the herbaceous plants in the vegetation, thereby reducing the full utilization of the habitat's resources (e.g., soil moisture); this "opening" of a formerly "closed" plant cover

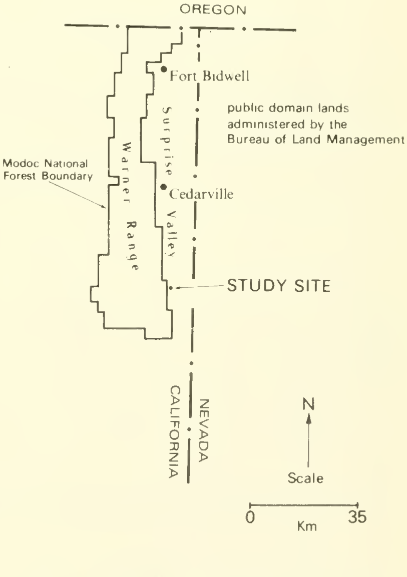

Fig. 1. The Warner Mountains area of extreme northeastern California.

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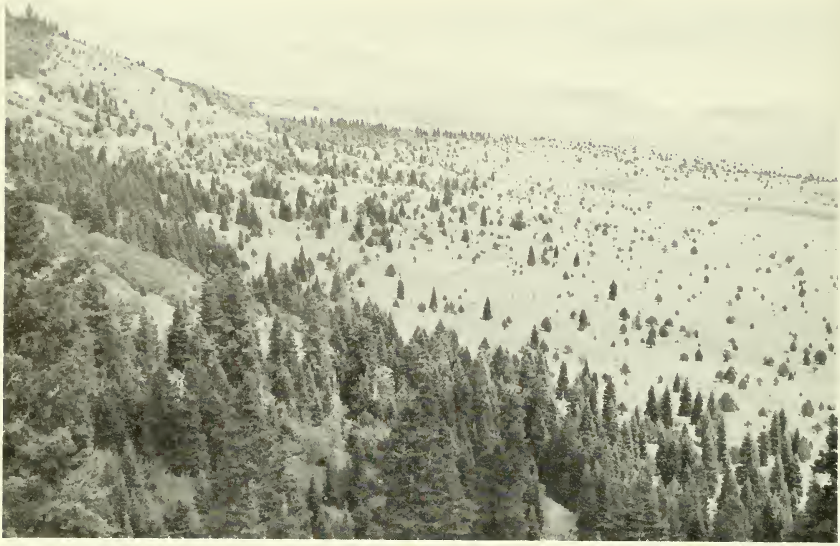

Fig. 2. Eastern slope of the Warner Mountains with the study area in the middle background.

may permit the establishment of species previously excluded (Robertson and Pearse, 1943). In a lodgepole pine invasion of grassy meadows, Vankat (1970) determined that most invasive trees were established immediately after, rather than during, a time of grazing by sheep. Trampling by the animals apparently killed seedling trees, but the heavy browsing and grazing did make the meadows susceptible to successful invasion after the sheep were removed.

Another cause sometimes invoked to explain tree advances into sagebrush is climatic fluctuation. Patten (1969) and Arnold et al. (1964) both suggest that, during abnormally wet periods, trees may become established in shrub environments typically too dry for them. Johnsen (1962) offers a variation on this theme by speculating that long droughts may initiate the invasion by reducing the cover of brush and herbaceous plants; when moist conditions return, trees are able to sprout and survive in the "opened" vegetation stand. This sequence of events is analogous to the "opening" of a "closed" plant community by livestock grazing.

Fire suppression is often invoked to explain the invasion of woody growth, usually trees, into grasslands in the southern Intermountain West (e.g., Foster, 1917; Pearson, 1931; Johnsen, 1962). Blackburn and Tueller (1970), moreover, suggest that a decrease in fires, together with overgrazing, accounts for the invasion of pinyon pine and juniper into brush in eastern Nevada. Abundant evidence exists suggesting that fires retard the spread of woody plants in the southern Intermountain West, although interpretation of tree invasion into sagebrush as a response to fire suppression is complicated by the fact that both the trees and the shrubs suffer from frequent fires.

METHODS

A site 35 km south of the town of Cedarville was selected for sampling the age structure of the young trees. The site appeared to be representative of the exposure, slope, and vegetation characterized by invading white fir in the southeastern Warner Mountains. Five plots, each 30 m by 60 m, were located at intervals of 0.5 km along the lower limit of young trees; an additional plot was located in a stand of young fir trees at a higher elevation where a southeastern exposure caused a higher forest-shrub transition. The selection of plots along the lower limit of these trees was designed to establish the period during which white fir invaded that portion of the area usually considered least hospitable to it. Within each plot, all trees greater than 20 cm dbh were cored with an increment borer, while the time elapsed since tree establishment was estimated to be eight years plus those indicated by the tree rings. Trees with diameters smaller than 20 cm were recorded by estimated height.

Results and Discussion

Although invasion began between 1915 and 1919, most white fir became established between 1925 and 1944 (Table 1). After 1944 a decrease in successful tree establishment is suggested by a gap in the age structure. More recent reproduction seems improved, judging from the relatively large number of trees between 0.5 and 2 meters in height. The absence of dead trees of any size precludes the possibility that older cohorts suffered mortality, an event which would complicate the determination of the initial tree invasion.

Climate.—The years correlated with the beginning of tree invasion constitute the driest period in the historical record, i.e., since the 1860s (Fig. 3). Consequently, the first white fir sprouted and survived, not when climatic conditions would have been most favorable for this

Table 1. Age structure of trees in sample plots and numbers of seedlings by height.

Trees whose diameters exceed 20 cm	
Year of establishment	Number of trees
Prior to 1915	0
1915-1919	1
1920-1924	1
1925-1929	6
1930-1934	8
1935-1939	10
1940-1944	6
1945-1949	2
1950-1954	1
1955-1959	4
Trees whose diameters are less than 20 cm	
Height in m	Number of trees
2-3	8
Less than 2	39

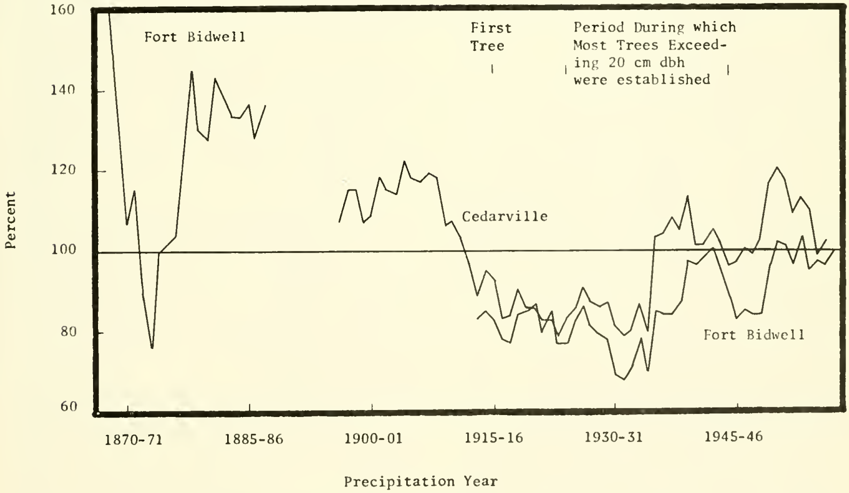

Fig. 3. Running five-year means of the percentage of average precipitation, based on precipitation years (1 July-30 June), for Cedarville and Fort Bidwell in Surprise Valley, California. Data source: U.S. Weather Bureau.

mesic species, but when drought should have hindered its establishment. The notion that dry conditions might have favored tree invasion by reducing the sagebrush-grass cover is untenable, because a drought so severe as to decrease the xeric sagebrush could not possibly simultaneously increase the mesic white fir.

The coincidence of drought and initial establishment of the white fir in this study, then, suggests that the trees invaded in spite of the weather rather than because of it. Moreover, it is apparent that nonclimatic factors prevented tree invasion during the more moist periods existing in the study area prior to 1910.

Fire suppression.— Although the Modoc Forest Reserve was established in 1904, wildfires in the Warner Mountains apparently continued to be common until after the creation of the Civilian Conservation Corps in 1933; the year 1924, for example, is reported to have been a particularly serious fire year (Cook, n. d.). More specifically, information from the U.S. Forest Service indicates that the area immediately adjacent to the study plots was burned by wild fires between 1921 and 1930, and that fires were common within the national forest during that decade (U.S. Forest Service, 1974). Supporting the impression that fire suppression was not well developed in the region by the time of tree invasion, the rangeland outside of the forest reserve, and in which the white fir became established, was not given official protection until passage of the Taylor Grazing Act in 1934. The Bureau of Land Management office in Susanville, California, out of which the federal rangelands in the region are administered, reports no records of fire suppression activities on the east slope of the Warner Mountains prior to 1950 (U.S. Bureau of Land Management, 1974).

The State of California was not, and is not, responsible for fire control in the study area, although it presently protects private rangelands west of the Warner Mountains (California Division of Forestry, 1975). Moreover, the state did not have any system for fire suppression during the initial years of tree establishment, and its fire protection policies cannot be considered to have been effective until after 1945 (Clar, 1969; Davis, 1965).

It seems valid to conclude that successful fire suppression on the east slope of the southern Warner Mountains was not effective until after the period of initial tree establishment. Although subsequent fire control has probably aided the maintenance of the trees, it cannot be invoked to explain the initiation of tree advance downslope.

Grazing.— The intensity of grazing by domestic livestock in the southeastern Warner Mountains has varied greatly since the initial settlement of Surprise Valley, immediately east of the Warner Range, in 1864. The number of cattle on ranches in Modoc County as a whole was little changed between 1890 and 1945, but it doubled in the following twenty years; resident sheep, by contrast, increased rapidly between 1890 and 1930, but by 1940 they had declined precipitously (Fig. 4).

Much of Modoc County is heavily forested, thus restricting grazing by domestic livestock to areas of brush or grass. Such habitats in the Warner Mountains and adjacent valleys have supported large numbers of animals, particularly sheep, over the last century. Contributing to the heavy grazing of these rangelands was the seasonal migration of sheep from the mountains in summer to the semiarid lowlands of northern Nevada in winter, a pattern well established by the 1870s (Olmsted, 1957). Moreover, sheep drives from Idaho and Oregon to shipping points in western Nevada passed through the Warner Mountains (Olmsted, 1957).

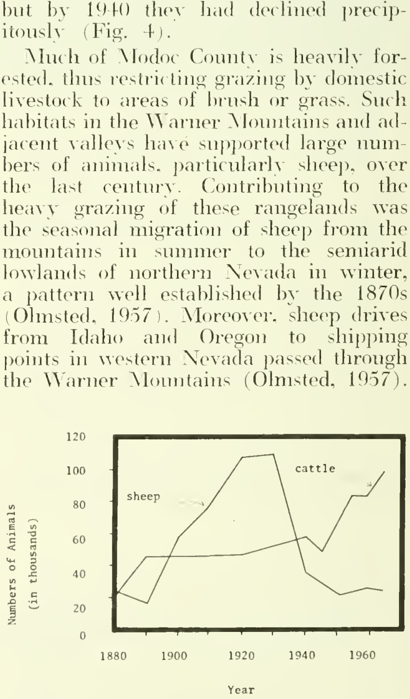

Fig. 4. Numbers of cattle and sheep on ranches in Modoc County. Data source: U.S. Bureau of Census.

By 1900 the ranges of Modoc County are said to have been greatly overgrazed (Brown, 1951; Pease, 1965).

Establishment of federal forest reserves (later to become national forests) in the early 1900s apparently did little to reduce immediately the grazing pressures in the higher elevations of Modoc County, including the Warner Mountains. Transient sheep continued to be driven across national forest land from Oregon until the Forest Service banned such use in 1914 (Tierney, 1946). Pease (1965) suggests that the elimination of grazing by transients prompted the establishment of new sheep ranches, with resident flocks, in Surprise Valley; this contributed to the rapid increase of resident sheep in Modoc County between 1910 and 1920. Also accentuating the heavy grazing pressures at this time, the Forest Service intentionally allowed overstocking on national forest lands in northeastern California during World War I to help meet war demands for food and wool; even after the war, heavy stocking continued because it was felt abrupt reductions in livestock numbers might have created economic hardship for area ranchers (Tierney, 1946).

Even while the national forest lands were under nominal regulation, the public domain continued to be completely free and open range. These latter federal lands in northwestern Nevada served, in part, as wintering grounds for sheep that were moved from California during the autumn season. Olmsted (1957) claims that 150,000 sheep were grazed in Surprise Valley in 1920, and, when compared to resident sheep reported on ranches in all of Modoc County in that year (109,000), it is apparent that much use of Surprise Valley ranges, including much public domain acreage, was by transient flocks. The peak in grazing pressure by sheep in the 1920s was apparently even greater than that suggested by the numbers of resident sheep.

The end of uncontrolled sheep grazing on the public domain came with the passage of the Taylor Grazing Act in 1934 (Olmsted, 1957; Pease, 1965). With more stringent regulations against transient flocks, the public lands could no longer be used by migratory sheep herders.

The grazing history suggests that the white fir invasion coincided with the peak, and the period immediately following the peak, of sheep grazing in the region. Sheep may have reduced the coverage of grass and shrubs, thereby increasing the availability of soil moisture and allowing the establishment of seedling trees. Sheep browse shrubs, but not conifers, on winter range, thus encouraging the tree invasion.

CONCLUSIONS

The evidence suggests that grazing by domestic livestock altered the sagebrush-grass vegetation on the east slope of the Warner Mountains and allowed the establishment of white fir seedlings. Yet, while grazing seems responsible for the initiation of tree invasion, the accelerated rate of tree establishment during the period 1935-1944 may have been the result of increased precipitation on the openings in the vegetation cover produced by grazing. Such an explanation would account for the decrease in tree establishment after 1944 because, by that time, the plant cover would have sufficiently recovered from the effects of the earlier heavy grazing to minimize the availability of suitable seedbeds and soil moisture. The cause of the present abundance of seedling trees is more obscure, but may be related to a resurgence of grazing pressure due to increasing numbers of cattle in recent years (Fig. 4).

In the northern Intermountain West generally, grazing by domestic livestock may be adequate to explain the widespread invasion of trees into sagebrush-grass vegetation during the late nineteenth and early twentieth centuries. The example from California, discussed in this paper, suggests that fire suppression has been too recent, except perhaps locally, to correlate with these tree invasions. (Control of fire may account for tree establishment in other vegetation types, however, during this time.) Regional climatic fluctuations, by themselves, also seem inadequate to account for the expansion of trees into sagebrush-grass vegetation during the latter half of the 1800s, a time characterized by "fluctuating but below average moisture" in western North America (Fritts, 1965). This portrayal of climate does not suggest conditions sufficiently wet to favor tree growth in formerly xeric brush. Moreover, tree invasion in the Warner Mountains began, not during a wet period, but during an extended time of below average precipitation. Grazing by domestic livestock, then, remains the most likely general cause, applicable on a regional basis, to account for the widespread invasion of sagebrush vegetation by tree species. Periods of extended drought may, in certain places, accentuate the plant cover deterioration caused by grazing, thus encouraging tree establishment once more moist conditions return.

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MORPHOLOGY OF EPHEMERAL AND PERSISTENT LEAVES OF THREE SUBSPECIES OF BIG SAGEBRUSH GROWN IN A UNIFORM ENVIRONMENT

W. T. McDonough, R. O. Harniss, and R. B. Campbell[1]

Abstract.- Measurements were made of morphological characteristics of ephemeral and persistent leaves of three subspecies of big sagebrush (*Artemisia tridentata* Nutt.) grown in a uniform environment. No morphological feature clearly separated the subspecies. Genetic-environmental interactions on leaf morphology apparently reduce its value as a sole criterion for distinguishing the subspecies.

Taxonomic subdivisions of a species may differ in morphological and physiological characteristics, and these differences may be genetically or environmentally controlled to varying extents. There is considerable interest in subspecies of big sagebrush (*Artemisia tridentata* Nutt.) because of differences in palatability, habitats occupied, and aggressiveness-characteristics of interest to range managers (McArthur et al., 1974). Identification is based chiefly on the growth form and morphology of leaves and on the inflorescence of plants collected from their normal habitats (Winward, 1970). Biochemical differences have also been noted in reproductive and vegetative parts (Winward and Tisdale, 1969; Hanks and Jorgensen, 1973; Stevens and McArthur, 1974). Biochemical patterns are less subject to environmental modification (Winward, A. H., 1975. Personal communication. Oregon State Univ., Corvallis) but are inconvenient for use in field indentification.

To determine the extent to which leaf morphology of big sagebrush subspecies is genetically rather than environmentally controlled, we grew plants of three subspecies under the same greenhouse conditions to identify distinguishing leaf characteristics that persist in a uniform environment.

Methods

Potted year-old plants of each of three subspecies, basin big sagebrush (*tridentata* Nutt.), mountain big sagebrush (*vaseyana* Rydb.), and Wyoming big sagebrush (*wyomingensis* Beetle), were established from seeds collected the fall of 1973 near the Sheep Experimental Range, Dubois, Idaho. The (25 cm) pots were randomly arranged on a greenhouse bench and given routine care. From the 50 plants of each subspecies, 6 plants and 10 mature leaves (ephemeral and persistent) from each plant were randomly selected for determinations of length, width, length/width, number and depth of lobes. Lobes were distinguished from occasional minor dentations by the presence of a secondary vein. Leaves were fixed to cards, photographed, and the 35-mm transparencies projected for measurements.

At the time of sampling, growing plants averaged 27 cm in height and had from 6 to 17 branches. Significance of differences at the 5 percent level was evaluated by variance analysis and multiple range tests.

Results

Representative leaves are shown in Figure 1; mean dimensions, in Table 1. Only limited differentiation was observed for both types of leaves among the subspecies.

In the ephemeral leaves, variation in lobe number was not significant. Width and length/width differed only in subsp. *vaseyana*. Subsp. *wyomingensis* differed from subsp. *tridentata* in lobe length and from subsp. *vaseyana* in lobe depth.

In the persistent leaves, length distinguishes subsp. *wyomingensis* from the other subspecies and length/width distinguishes *wyomingensis* from *tridentata*. Number of lobes was uniformly three in all subspecies, and lobing generally was so shallow that attempted measurements were unreliable.

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TABLE 1. Mean dimensions[1] ± standard deviations of leaves of three subspecies of big sagebrush grown in a uniform environment.

Subspecies	Length (mm)	Width (mm)	Length/Width	Number of lobes	Lobe depth (mm)
			Ephemeral Leaves		
Tridentata	50.9^{a} ±7.1	19.3^{a} ±6.8	3.0^{a} ±1.2	4.0^{a} ±1.1	9.8^{ab} ±3.7
Vaseyana	47.9^{ab} ±5.4	15.6^{b} ±5.9	3.6^{b} ±1.8	3.8^{a} ±0.9	8.4^{b} ±3.4
Wyomingensis	43.3^{b} ±4.7	19.6^{a} ±6.1	2.5^{a} ±1.0	4.0^{a} ±1.0	11.4^{a} ±3.6
			Persistent Leaves		
Tridentata	14.3^{a} ±2.5	3.1^{a} ±0.7	4.9^{a} ±1.2	3^{a}	—
Vaseyana	14.9^{a} ±3.0	3.4^{a} ±0.7	4.5^{ab} ±0.6	3^{a}	—
Wyomingensis	11.9^{b} ±2.3	3.0^{a} ±0.8	4.1^{b} ±0.8	3^{a}	—

[1] Means for any measurement with the same letter in superscript do not differ significantly.

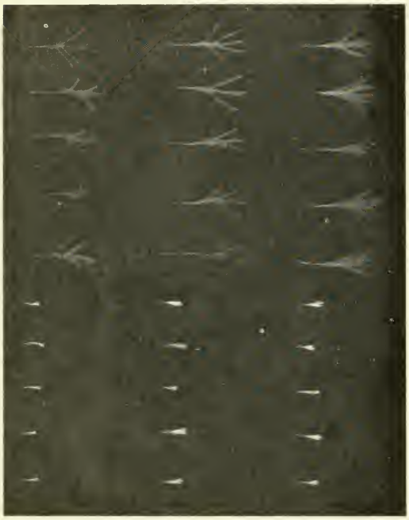

Fig. 1. Ephemeral (above) and persistent (below) leaves of sagebrush grown in a uniform environment subsp. tridentata (T), vaseyana (V), and wyomingensis (W).

Winward (1970) examined only persistent leaves of field-grown plants. Only differences in length/width were considered useful in separating the subspecies. Values of 5.6, 4.0, and 3.1 were assigned, respectively, to subsp. *tridentata*, *vaseyana*, and *wyomingensis*. Leaves of plants grown under uniform conditions are in the same sequence but have somewhat divergent values that do not differentiate subsp. *vaseyana* (Table 1).

CONCLUSIONS

Even with careful measurements, no characteristic of ephemeral or persistent leaves from plants grown under uniform conditions was found to clearly separate the three subspecies. Only subsp. *vaseyana* is distinguishable by two characteristics of ephemeral leaves and subsp. *wyomingensis* by one characteristic of persistent leaves. Distinguishing leaf morphology may be so dependent upon environmental modification that it is not uniformly useful in identification. Alternatively, distinct morphological differences may be obscured by genetic introgression among subspecies and hybrids (Plummer, A. P., 1975. Personal communication. U.S. Dep. Agric. For. Serv., Intermt. For. and Range Exp. Stn., Ogden, Utah) or because insufficient numbers of plants are sampled from the same or other areas.

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The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

VOLUME 35 December 31, 1975 No. 4

ENDANGERED, THREATENED, EXTINCT, ENDEMIC, AND RARE OR RESTRICTED UTAH VASCULAR PLANTS

Stanley L. Welsh[1], N. Duane Atwood[2], and James L. Reveal[3]

ABSTRACT.— The status of 382 vascular plant taxa with distribution in Utah is presented. Some 66 species are possibly endangered, 198 threatened, 7 extinct, and 20 extirpated within the state; 4 species have questionable taxonomic status. Included in the list are nearly 225 species of endemic plants, many of which are among the possibly endangered, threatened, and extinct or extirpated plants. Bibliographic citations, type locality, status, and distribution by counties is included for each species or infraspecific taxon. Two new species are described: *Psoralea pariensis* and *Eriogonum natum*. One new name, *Astragalus barnebyi*, is proposed; and one new variety, *Eriogonum umbellatum* var. *deserticum*, is proposed. The following new combinations are made: *Cycladenia humilis* var. *jonesii; Aralia racemosa* ssp. *bicrenata; Heterotheca jonesii; Hymenoxys depressa; Xanthocephalum sarothrae* var. *pomariense; Thelypodium integrifolium* var. *complanatum; Thelypodium sagittatum* var. *ovalifolium; Arenaria kingii* var. *plateauensis; Psorothamnus thompsonae; Najas caespitosus; Oenothera gouldii; Eriogonum corymbosum* var. *revealianum; Penstemon humilis* var. *obtusifolius; Penstemon lentus* var. *albiflorus;* and *Viola purpurea* var. *charlestonensis*.

The vascular plant flora of Utah is both large and complex. Its components are diverse, representing numerous floristic elements from many parts of North America, including unique and provincial elements restricted to the state. Species of many major geographical groupings of plants occur within the multiplicity of habitats available within Utah, all to a greater or lesser degree of their entire range. Some of these species are at the edge of their total range, and these occur in smaller portions of the state. Other taxa occur only in one or few peculiar, limited edaphic situations or habitats, while others are more widespread and cover a broad altitudinal or latitudinal expanse of Utah.

Those plants that occur only within the state, or within the natural basins that overlap the artificial political boundaries of the state, are known as local endemics. Their range can be widespread within Utah, but more often they are restricted in distribution to very limited areas. These are plants that are of much interest to scientists, because they present living proof of the origin and evolution of species, origin of floras, and indications of relationships of plant species. These plants are those entities which have originated here or are mere remnants of species which have had a much broader area of distribution in the past.

The impress of man and his activities onto the natural habitats of Utah has reduced the area available to most native or indigenous plants. Those species of broad extent and wide ecological tolerances have withstood these activities best, with only a reduction in their range and number. Less frequently their range has increased in size as less-tolerant plants of adjoining areas have been reduced. However, many of the most unique species have areas of distribution that are very small, with only a few known individuals. In some examples the species have apparently ceased to exist in the Utah flora. In most cases the new habitats made available by the activities of man have been occupied by introduced, cultivated, and adventive plants from the Old World. These are the crop plants and weeds of modern agricultural and industrial society.

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The phalanxes of intolerant native plants have been retreating under the impacts of agriculture and grazing for more than a century. Industrial development during most of that period was limited in extent, if not in effect. In Utah most of these activities were restricted mainly to the broad valleys and river basins, where plant communities that were relatively fragile are now almost totally lacking within the state. However, these sites apparently contained few of the narrowly endemic plant species. With the advent of the second half of the twentieth century, there has occurred a resurgence of economic activities, mineral exploration, and a greater use of the public lands which hitherto had been considered as useful (if considered useful at all) only for grazing and watershed. The rapid spread of industrial development into previously undeveloped, low-elevation, arid lands in the southern portions of the state is all the more impressive when one considers that most of the narrowly restricted plants occur in those areas (Figs. 1 and 2). Plant species which were once remote from the impacts of civilization—industrial, agricultural, or recreational activities—are now threatened not only by the effects of ranching, construction, and off-road travel, but even by the very agencies of government which are established by law to oversee in the public trust the proper use and protection of the public lands. At the present time, hardly a part of Utah, even that set aside as national parks, monuments, or wilderness areas, is safe from degradation by masses of people or by those seeking to exploit the very natural resources and features these unique areas were established to protect.

Inroads into the most remote and most arid portions of the state now guarantee further reduction of the unique flora of Utah. Naturally, those entities that will suffer greatest from the commercialization of the state will be those which have specific and naturally restricted areas of

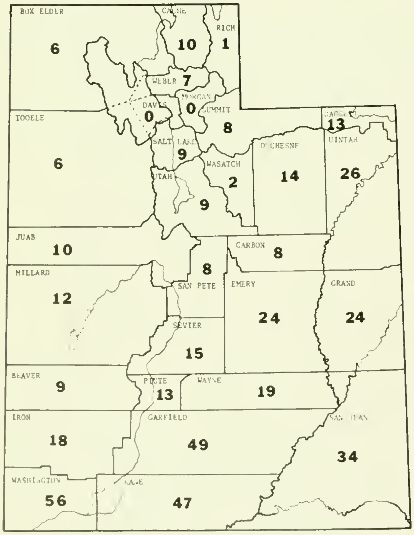

Fig. 1. Distributional incidence of endangered, threatened, extinct, or extirpated Utah plants by county; total number is greater than the total for the state due to overlap.

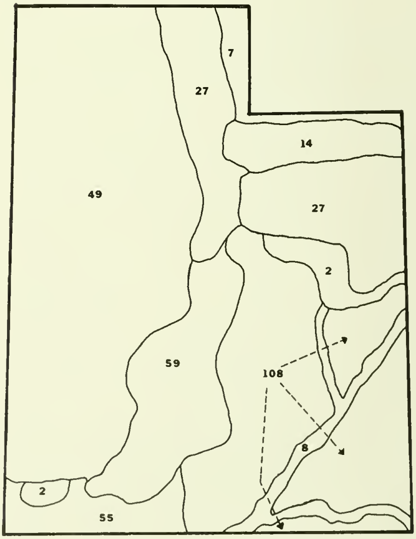

Fig. 2. Distribution of endangered, threatened, extinct, and rare or restricted Utah plants, by phytogeographical subdivision.

distribution. Only the most enlightened management and protection from unreasonable exploitation will ensure the continuation of the rich indigenous flora that these plants represent.

Commerical exploitation need not bring about the demise of species, although the basic nature of the flora will change. It is a fact of biology that in even the most enlightened and carefully planned development, there will be a reduction in the native vegetation. Reclamation attempts will be made with Old World introductions, or with selected ecotypes of indigenous plants, and not with those that occurred in the region prior to its modification. Both of these types of plants can hardly replace the quality of those cleared and destroyed by construction activities. Revegetation of a disturbed site can be more or less productive from an economic standpoint, but natural plant succession will require generations before any real resemblance of the natural vegetation will again be possible, and then, depending on the nature of the disturbance, the native vegetation occupying the site can be of an entirely different composition than formerly. Indigenous taxa with specific habitat requirements will not survive if those habitats are altered, and there is no known technology which can simulate some of the peculiar habitats present in the state—which are now occupied by narrowly restricted plants—and no technology can ever replace an extinct species (Reveal 1973b).

Because of the rate at which Utah is being impressed by all the forces of a modern society, it seems important that the endangered, threatened, extinct, endemic, and rare or restricted vascular plants of Utah be inventoried, and that their known or historic areas of distribution be outlined. That task is the basic goal of this paper, but this is only a pioneering effort. Much work remains to be done.

While the present paper was in preparation, the secretary of the Smithsonian Institution, S. Dillon Ripley, transmitted to the Congress of the United States a "report on endangered and threatened species of the United States." This report (cited herein as "Ripley 1975") lists numerous plants from Utah as either threatened, endangered, possibly extinct, or probably extinct. Each category was abbreviated as T, E, PoEx, or PrEx, respectively.

That report was prepared during the calendar year of 1974 as mandated by the Endangered Species Act of 1973 (Public Law 93-205) in which the secretary of the Smithsonian was to report to Congress within one year on all of the "species of plants which are now or may become endangered or threatened" in the United States (sec. 12). The Congress provided no funding for the preparation of this report, and the time restrictions prevented a detailed field examination of all species included in the list. Some states, notably California and Texas, with active offices concerned with endangered plant species, were able to provide precise data; other states were able to supply some information, and still others had little or no input into the final report, except that gathered by the committee established by the secretary to prepare a statement for the Congress. The data for the state of Utah was provided by a number of individuals (including the authors of this paper, and Reveal served on the Smithsonian committee), but time did not permit the type of critical examination of each taxon which has been largely possible for the present paper. The Smithsonian report (Ripley 1975) was published in the Federal Register (Schreiner 1975) as a "notice of consideration," and we understand that the Department of Interior will submit a revised listing in the near future. Disagreement as to the designation of degree of endangerment between this paper and that of Ripley (1975) represents the results of a more detailed and concentrated survey of the Utah flora, and is based on detailed literature search and personal information of the present authors and that of their colleagues who have reviewed the manuscript. These differences have largely been resolved and will appear in the Smithsonian's revised list to be submitted early in 1976 to the Secretary of the Interior. Much of the information has been acquired through many years of investigation of the Utah flora, both in the field and in the herbarium, and has been stimulated by the Ripley (1975) report.

The designation of the status of an individual taxon as belonging to a particular category is subjective. Still, it is based on the best information available to us at the present time (a requirement of the Endangered Species Act). A plant species is considered as "endangered" when its known area of distribution is very small, and when the expected development or exploitation of the area occupied has already occurred or is imminent. A "threatened" plant is one of somewhat larger known areal extent, but which has experienced or is now experiencing a reduction of its natural distributional area. These are the two major categories required by law to be designated. Plants that are "rare or restricted" are those which have been collected only occasionally or which are known from very limited regions of the state; they may or may not be widely distributed elsewhere outside the political confines of Utah. Introduced species are excluded from this category, even though they might be restricted or even rare.

Plants considered to be "endemic" are those whose entire distributional area is within Utah or within one of the natural drainage basins which overlap the political boundaries of the state. Some plants in this category especially are poorly known taxonomically and biologically, and in these cases we have so indicated the need for a careful systematic evaluation of the taxon to determine the status of the plant entity.

All statements about status of those plants not endemic to Utah are with regard to the occurrence of those plants within Utah. In many, if not most of these cases, the species are widespread and common to abundant in other portions of their area of distribution. If they are limited, rare, or possibly extirpated from Utah, only that portion of their range is considered in making the designation. This follows the guidelines established by California and Texas in which the endangered and threatened lists are based solely upon the situation of the plant in question within the confines of the state boundaries (Table 1).

Plants listed in one of the categories designated above by Ripley (1975) are included here, whether or not they are considered as something other than threatened, endangered, or extinct on the new list that will be published in 1976. Obvious errors, which will not be repeated in the future, such as *Lewisia maguirei* and *Penstemon decurvus*, to mention only two, are excluded.

Voucher specimens for some of the reports are cited in the distribution statements (e.g., *Harrison 6370*, for *Cymopterus basalticus*). Bibliographic citations in support of distributional data are included for many species, especially for those which are obscure or are poorly represented in herbaria. We are not making any attempt to provide precise location data (except as might be obtained from published type localities) in fear of commercial exploitation of some plants (i.e., catci and orchids) and because of the possibility of destruction of selected populations by those having a vested interest in ridding parcels of land of any species of plant that might fall under the protection of the provisions of the Endangered Spe-

TABLE 1. Numerical summary of the endangered, threatened, extinct, extirpated and rare or endemic species in Utah.

County	Endangered	Threatened	Extinct	Extirpated	Rare/Endemic
Beaver	1	7	0	1	11
Box Elder	1	5	0	0	1
Cache	2	8	0	0	3
Carbon	2	6	0	0	11
Daggett	3	9	0	1	4
Davis	0	0	0	0	4
Duchesne	3	9	1	1	14
Emery	4	19	1	0	28
Garfield	9	39	1	1	38
Grand	6	17	0	1	30
Iron	2	15	1	0	9
Juab	0	7	0	3	10
Kane	12	31	0	4	26
Millard	2	9	1	0	14
Morgan	0	0	0	0	0
Piute	0	12	0	1	8
Rich	1	1	0	0	1
Salt Lake	0	8	0	1	8
San Juan	7	25	0	2	27
Sanpete	1	6	1	0	9
Sevier	2	13	0	0	7
Summit	2	3	0	3	6
Tooele	0	3	0	3	7
Uintah	7	17	1	1	14
Utah	1	7	0	1	13
Wasatch	0	1	1	0	5
Washington	12	41	0	3	24
Wayne	5	14	0	0	29
Weber	0	7	0	0	4

cies Act of 1973. Nevertheless, those agencies charged with protection of endangered or threatened plants must determine the precise localities of those entities in order to plan for their survival.

Maps are presented (Figs. 1 and 2) which demonstrate the unequal distribution of these unusual plants. In Figure 1 the number of taxa known of each county is indicated. The total appears to be very large, but this is due to many of the species being listed in several counties when area of distribution occurs outside a single county. Phytogeographic regions of Utah are plotted in Figure 2, and the number of taxa considered to be unusual is cited for each. The number of taxa totals are less than for the entire state because some distributional data are so indefinite as to not be plotable. Also, the figures represent an attempt to plot plants within their main area of distribution; double representation has been avoided. This accounts for the apparent discrepancies between the two maps.

Recommendations

Land use planning should take into account the presence of the unusual plants present in the state of Utah. If and when the Secretary of Interior proclaims any species of plants found in Utah as endangered or threatened, they will fall under the protective provisions of the Endangered Species Act which, in section seven, calls upon all federal departments and agencies "to insure that actions authorized, funded, or carried out by them do not jeopardize the continued existence of such endangered species and threatened species or result in the destruction or modification of habitat of such species." Those which are protected by law must be determined, and their areas of distribution should become known to the agencies responsible for their protection. Questionable taxonomic units should be investigated in order to determine their nature and area of distribution. Plants thought to be extinct should be sought in carefully coordinated field studies. The results of these studies should be reported to the Secretary of the Interior so that information about the various species may be updated from time to time, and so the status of each taxon can be reviewed. When new species are described from Utah, their status should be evaluated, and if they should prove to be endangered or threatened, that information should be presented to the Secretary so that such species may be considered for the federal endangered species list.

In a recent issue of the Federal Register, Greenwalt (1975) proposed a "rulemaking" for various amendments to the Endangered Species Act of 1973. These amendments introduce the term "plant" into many sections of the act. However, as Lachenmeier (1974) has pointed out, there are several legal and constitutional questions about the act that need to be resolved still, and from a botanical point of view, there still exist certain discriminatory differences between "wildlife" and "plants." These must be resolved in the future.

In and for the state of Utah, we recommend that a review board be appointed to oversee the protection of Utah's most unique plants, and funding should be forthcoming to allow a real understanding not only of the endangered and threatened species, but the entire state's flora. The state should adopt the federal act and include within its own listing those species of the state which are endangered or threatened within its borders. Policies should be adopted that will determine basic land use with regard to these unique plants, and "critical habitats" as provided by the act should be investigated throughout the state (see also Greenwalt & Gehringer 1975). Above all, prompt actions must be taken by the state to preserve and protect the state's unique flora, and the members of the botanical community must be ready to aid and assist all levels of government in this important endeavor.

Note

In the following list, we are abbreviating journals according to the abbreviations listed by Lawrence et al. (1968) and herbaria according to listing given by Holmgren and Keuken (1974). We have attempted to give the type information as published in the original place of publication; however, we are not attempting to typify any name, nor is the herbarium cited considered a statement of lectotypification. This information is given for the convenience of the reader. For the most part, the abbreviations of the authors follow the unpublished suggestions of the Index Kewensis staff.

Acknowledgments

The authors wish to acknowledge the critical reviews supplied by our colleagues in the study of Utah's plant taxonomy. Especially important help and criticism was supplied by Arthur H. Holmgren, Lois Arnow, and Andrew H. Barnum.

Apiaceae

Angelica wheeleri S. Wats., Amer. Naturalist 7: 301. 1873.

Type: Utah, *Wheeler s.n.* (gh).

Status: Endemic, evidently rare and local, possibly threatened.

Distribution: Northern and central Utah (Mathias & Constance 1945).

Cymopterus basalticus M. E. Jones, Contr. W. Bot. 12: 6. 1908.

Type: Half-way Station, west of Wa Wa, Millard or Beaver Co., Utah, 7,000 feet, 15 May 1906, *M. E. Jones s. n.* (pom).

Status: Restricted and locally abundant, neither threatened nor endangered (Ripley, T).

Distribution: Western Utah (Millard Co., *Harrison 6370; Matthews 14* [bry]), and adjacent Nevada (Mathias & Constance 1945).

Cymopterus coulteri (M. E. Jones) Mathias, Ann. Missouri Bot. Gard. 17: 276. 1930, based on *C. corrugatus* var. *coulteri* M. E. Jones, Contr. W. Bot. 12:19. 1908.

Type: Juab, Juab Co., Utah, 4,000 feet, 30 Apr 1880, *M. E. Jones 1691* (us).

Status: Endemic, rare and restricted, threatened (Ripley, T).

Distribution: Western Utah (Sanpete Co., *Mabey 5300* [bry]).

Cymopterus duchesnensis M. E. Jones. Contr. W. Bot. 13: 12. 1910.

Type: Among loose rocks on southern slopes of mesas, Myton, Duchesne Co., Utah, 5,000 feet, 20 May 1908, *M. E. Jones s.n.* (pom).

Status: Endemic, rare and restricted, threatened (Ripley, E).

Distribution: Duchesne and Uintah counties, Utah (*Welsh 180* [bry]; *Holmgren & Reveal 1887* [ny, utc]; *Holmgren & Holmgren 5169* [bry, ny, utc]).

Cymopterus jonesii Coult. & Rose, Rev. N. Amer. Umbell. 80. 1888.

Type: Frisco, Beaver Co., Utah, 8,000 feet, 22 Jun 1880, *M. E. Jones 1808* (US).

Status: Rare and restricted.

Distribution: Southwestern Utah and Nevada (Mathias & Constance 1945).

Cymopterus higginsii Welsh, Great Basin Nat. 35: 377. 1976.

Type: Shadscale dominated bajada, on gravelly pedimental fan east of None Butte, ca 17 miles east of Glen Canyon City, Kane Co., Utah, 31 May 1975, *S. L. Welsh 12740* (bry).

Status: Endemic, local; possibly threatened.

Distribution: Eastern Kane Co., Utah.

Cymopterus minimus (Mathias) Mathias, Brittonia 2: 245. 1936, based on *Aulospermum minimum* Mathias, Ann. Missouri Bot. Gard. 17: 353. 1930.

Type: On the upper part of the "Breaks" at Cedar Breaks, Iron Co., Utah, ca 10,500 feet, *Mathias 723* (mo).

Status: Endemic, rare and restricted to Cedar Breaks, possibly endangered (Ripley, E).

Distribution: Cedar Breaks, Iron Co., Utah.

Cymopterus newberryi (S. Wats.) M. E. Jones, Zoe 4: 47. 1893, based on *Peucedanum newberryi* S. Wats., Proc. Amer. Acad. Arts 11: 145. 1876.

Status: Widespread and at least locally abundant, neither threatened nor endangered (Ripley, T).

Distribution: Garfield, Grand, Kane, Millard, San Juan, Uintah, Washington, and Wayne counties, Utah (bry, utc), and northern Arizona (Mathias & Constance 1945).

Cymopterus rosei M. E. Jones, Contr. W. Bot. 12: 17. 1908.

Type: Richfield, Sevier Co., Utah, 18 Jun 1898, *M. E. Jones 30* (us).

Status: Endemic, rare and local, possibly threatened (Ripley, T).

DISTRIBUTION: Iron, Sanpete, Sevier, and Washington counties, Utah (*Maguire 19131; Holmgren 10932* [UTC]).

Ligusticum porteri Coult. & Rose var. *brevilobum* (Rydb.) Mathias & Constance, Bull. Torrey Bot. Club 68: 123. 1941, based on *L. brevilobum* Rydb., Fl. Rocky Mts. 613, 1064. 1917.

TYPE: Aquarius Plateau, Utah 5 Aug 1905, *Rydberg & Calrton 7473* (NY).

STATUS: Endemic, rare and local; possibly threatened.

DISTRIBUTION: Aquarius Plateau, Garfield Co., Utah (Mathias & Constance 1941).

Lomatium latilobum (Rydb.) Mathias, Ann. Missouri Bot. Gard. 25: 281. 1937, based on *Cynomarathrum latilobum* Rydb., Bull. Torrey Bot. Club 40: 73. 1913.

TYPE: Proposed dam site, near Wilson Mesa, Grand Co., Utah, *Rydberg & Garrett 8371* (NY).

STATUS: Endemic, rare and local, possibly threatened.

DISTRIBUTION: Grand Co., Utah (BRY; UTC).

Lomatium megarrhizum (A. Nels.) Mathias, Ann. Missouri Bot. Gard. 25: 282. 1937, based on *Peucedanum megarrhiza* A. Nels., Bull. Torrey Bot. Club 26: 130. 1899.

STATUS: Rare and local, possibly threatened.

DISTRIBUTION: Emery Co., Utah (*Higgins 1268* [BRY]) and southwestern Wyoming (Mathias & Constance 1945; Higgins 1972b).

Lomatium minimum Mathias, Ann. Missouri Bot. Gard. 25: 273. 1937.

TYPE: Near the hotel, on dry slopes bordering Bryce Canyon, Garfield Co., Utah, 8,600 feet, *Mathias 670* (MO).

STATUS: Endemic, local, possibly threatened (Ripley, T).

DISTRIBUTION: Garfield, Iron, and Kane counties, Utah (BRY, UTC).

Lomatium scabrum (Coult. & Rose) Mathias, Ann. Missouri Bot. Gard. 25: 275. 1937, based on *Cynomarathrum scabrum* Coult. & Rose, Contr. U.S. Natl. Herb. 7: 247. 1900.

TYPE: Frisco, Beaver Co., Utah, 2,400 meters, *Jones 1864* (US).

STATUS: Endemic (but possibly in Mohave Co., Arizona), locally common, not threatened nor endangered.

DISTRIBUTION: Beaver, Iron (UT), Millard, and Washington counties, Utah (BRY).

Musineon lineare (Rydb.) Mathias, Ann. Missouri Bot. Gard. 17: 265. 1930, based on *Daucophyllum lineare* Rydb., Bull. Torrey Bot. Club 40: 69. 1913.

TYPE: Near Logan, Cache Co., Utah, 9 Aug 1895, *Rydberg s.n.* (NY).

STATUS: Endemic, possibly threatened.

DISTRIBUTION: Cache Co., Utah (*Holmgren 3595* [UTC]).

APOCYNACEAE

Cycladenia humilis Benth. var. *jonesii* (Eastw.) Welsh & Atwood, stat. et comb. nov., based on *C. jonesii* Eastw., Leafl. W. Bot. 3: 159. 1942.

TYPE: San Rafael Swell, Emery Co., Utah, 19 May 1914, *M. E. Jones s.n.* (CAS).

STATUS: Endemic, rare and endangered (Ripley, E).

DISTRIBUTION: Emery and Grand counties, Utah.

This entity is known in Utah from three basic collections: the type as cited above, a collection by Cottam (UT) also from the San Rafael Swell, and a collection from Castle Valley, Grand Co., Utah (Welsh 1970b).

ARALIACEAE

Aralia racemosa L. ssp. *bicrenata* (Wooton & Standley) Welsh & Atwood, stat. & comb. nov., based on *A. bicrenata* Wooton & Standley, Contr. U.S. Natl. Herb. 16: 157. 1913.

STATUS: Rare; restricted to Zion Narrows, Washington Co., Utah.

DISTRIBUTION: Washington Co., Utah (*Welsh 12366* [BRY]), and from southeastern Canada south to Georgia, westward to Arizona and northern Mexico (Kearney & Peebles 1951); the subspecies is from Utah and Arizona.

ASCLEPIADACEAE

Asclepias cutleri Woodson, Ann. Missouri Bot. Gard. 26: 263. 1939.

STATUS: Rare, threatened.

Distribution: Grand (*Cottam 5799* [BRY] and San Juan (*Holmgren 3144* [UTC]) counties, Utah, and from northeastern Arizona.

Asclepias engelmanniana Woodson, Ann. Missouri Bot. Gard. 28: 207. 1941.

Status: Rare.

Distribution: Grand (*Rydberg & Garrett 8504* [UT]) and San Juan (*Welsh et al. 2930* [BRY]) counties, Utah; from Nebraska to Texas and Arizona.

Asclepias labriformis M. E. Jones, Proc. Calif. Acad. Sci. II, 5: 708. 1895.

Type: Capital Wash, near the Henry Mts., Wayne Co., Utah, 5,000 feet, in sandy gulch, 19 Jul 1894, *M. E. Jones 5650* (POM).

Status: Endemic to the state but common, neither threatened nor endangered.

Distribution: Emery, Garfield, San Juan, Uintah, and Wayne counties, Utah (BRY).

Asclepias ruthiae Maguire & Woodson, Ann. Missouri Bot. Gard. 28: 245. 1941.

Type: Frequent, sandy soil, vicinity of water tanks, Calf Spring Canyon, 5,000 feet, San Rafael Swell, 18 miles southeast of Castle Dale, Emery Co., Utah, 10 May 1940, *Maguire & Maguire 18310* (UTC).

Status: Endemic, common in disjunct populations on the San Rafael Swell; possibly threatened (Ripley, T).

Distribution: Emery (*Cottam 5500*, *Harrison 8067*, *Higgins & Reveal 1285a* [BRY], *Grand* [see Woodson 1954), and Wayne (*Harrison 11223* and *11891* [BRY]) counties, Utah.

Asteraceae

Chamaechaenactis scaposa (Eastw.) Rydb., Bull. Torrey Bot. Club 33: 156. 1906, based on *Chaenactis scaposa* Eastw., Zoe 2: 231. 1891.

Status: Restricted, rare except locally, not threatened nor endangered.

Distribution: Carbon, Duchesne, Emery, San Juan, Uintah, and Wayne counties, Utah, and western Colorado (BRY, UTC).

Cirsium rydbergii Petrak, Beih. Bot. Centralbl. 35 (2): 315. 1917.

Type: Along the San Juan River near Bluff, San Juan Co., Utah, 1,200-1,500 meters, 1-2 Jul 1911, *Rydberg 10001* (G?).

Status: Habitat specific, in hanging gardens, restricted and possibly threatened.

Distribution: Garfield, Grand, Kane, San Juan, and Wayne counties, Utah (BRY), and Black Mesa, Apache Co., Arizona (Howell & McClintock 1960).

Enceliopsis nutans (Eastw.) A. Nels., Bot. Gaz. 47: 433. 1909, based on *Encelia nutans* Eastw., Zoe 2: 230. 1891.

Status: Habitat specific, in heavy clay soils, restricted and rare.

Distribution: Carbon, Duchesne, Emery, Grand, Uintah, and Wayne counties, Utah (BRY, UTC), and western Colorado (Harrington 1954).

Erigeron abajoensis Cronq., Brittonia 6: 168. 1947.

Type: Abajo Mts. (eastern range), 3,000-5,300 meters, San Juan Co., Utah, 17 Aug 1911, *Rydberg & Garrett 9755* (NY).

Status: Endemic, rare and threatened (Ripley, T).

Distribution: Garfield, Kane, and San Juan counties, Utah (BRY).

Erigeron arenarioides (D. C. Eaton) Rydb., Fl. Rocky Mts. 1067. 1917, based on *Aster arenarioides* D. C. Eaton ex A. Gray, Proc. Amer. Acad. Arts 8: 647. 1873.

Type: Rocky gulch above Cottonwood Canyon, Wasatch Mountains, Salt Lake Co., Utah, 8,000-9,000 feet, Aug 1869, *Waston 547* (US).

Status: Endemic and rare, restricted to rock crevices, threatened.

Distribution: Salt Lake, Tooele, Utah, and Weber counties, Utah (BRY, UTC; Cronquist 1947).

Erigeron cronquistii Maguire, Brittonia 5: 201. 1944.

Type: Cliffs, north side of Logan Canyon 1/4 mile below forks, Bear River Range, Cache Co., Utah, 5,800 feet, 20 May 1939, *Maguire 16681* (NY).

Status: Endemic, rare and threatened (Ripley, T).

Distribution: Cache Co., Utah (Cronquist 1947).

Erigeron garrettii A. Nels., Manual Bot. Centr. Rocky Mts. 526. 1909.

TYPE: Big Cottonwood Canyon, Salt Lake Co., Utah, 28 Jun 1905, *Garrett 1310* (RM).

STATUS: Endemic, rare and possibly threatened (Ripley, T).

DISTRIBUTION: High altitudes in Box Elder (UT), Salt Lake and Utah counties, Utah (BRY; Cronquist 1947).

Erigeron flagellaris A. Gray var. *trilobatus* Maguire ex Cronq., Brittonia 6: 258. 1947.

TYPE: Canyon to Cedar Breaks, 12 miles east of Cedar City, Iron Co., Utah, 5 Aug 1934, *Maguire 14947* (NY).

STATUS: Endemic and rare, endangered (Ripley, E).

DISTRIBUTION: Iron Co., Utah; known only from the type locality (Cronquist 1947).

Erigeron kachinensis Welsh & Moore, Proc. Utah Acad. Sci. 45: 231. 1968.

TYPE: Hanging gardens and seeps, near Kachina Natural Bridge, Natural Bridges N.M., San Juan Co., Utah, 13 Aug 1963, *Welsh & Moore 2398* (BRY).

STATUS: Endemic, rare and endangered (Ripley, E).

DISTRIBUTION: San Juan Co., Utah; known only from the type locality (Welsh & Moore 1968).

Erigeron maguirei Cronq., Brittonia 6: 165. 1947.

TYPE: Dry rocky sandy canyon bottom, Calf Spring Wash, 1.5 mile up San Rafael Swell, 16 Jun 1940, 5,500 feet, *Maguire 18459* (NY).

STATUS: Endemic, rare and possibly extinct (Ripley, E).

DISTRIBUTION: Emery Co., Utah; known only from the type locality.

Erigeron mancus Rydb., Fl. Rocky Mts. 902, 1067. 1917.

TYPE: LaSal Mts., Grand or San Juan Co., Utah, 7 Jul 1911, *Rydberg & Garrett 8671* (NY).

STATUS: Endemic, rare and possibly threatened (Ripley, T).

DISTRIBUTION: LaSal Mts., Grand and San Juan counties, Utah (Cronquist 1947.)

Erigeron religiosus Cronq., Brittonia 6: 258. 1947.

TYPE: Clear Creek, Zion N.P., Washington Co., Utah, 8 Sep 1938, *Eastwood & Howell 6339* (CAS).

STATUS: Endemic, rare and endangered (Ripley, E).

DISTRIBUTION: Kane (*Harrison 11085* [BRY] and Washington counties, Utah (Cronquist 1947).

Erigeron sionis Cronq., Brittonia 6: 258. 1947.

TYPE: Zion N.P., Washington Co., Utah, 1-3 Aug 1925, *Pilsbry s.n.* (PH).

STATUS: Endemic, very rare and endangered (Ripley, E).

DISTRIBUTION: Washington Co., Utah; known only from type locality.

Flaveria campestris J. R. Johnston, Proc. Amer. Acad. Arts 29: 287. 1903.

STATUS: Rare, restricted, but not apparently threatened or endangered.

DISTRIBUTION: Grand Co., Utah (Maguire 1937; Harrison et al. 1964); Colorado, New Mexico and northern Mexico.

Gaillardia flava Rydb., N. Amer. Fl. 34: 139. 1915.

TYPE: Lower Crossing of the Price River (see Jones 1965), Emery Co., Utah, 2 Jul 1898, *M. E. Jones 6412* (US).

STATUS: Endemic, rare and endangered.

DISTRIBUTION: Emery Co., Utah (*Cottam & Hutchings 2176* [BRY]).

Gaillardia spathulata A. Gray, Proc. Amer. Acad. Arts 12: 59. 1876.

TYPE: Rabbit Valley, Wayne Co., Utah, 7,000 feet, 1875, *Ward s.n.* (GH).

STATUS: Endemic, common throughout its range, neither threatened nor endangered.

DISTRIBUTION: Carbon, Emery, Garfield, Grand, and Wayne counties, Utah (BRY, UTC).

Haplopappus scopulorum (M. E. Jones) Blake in Tidestrom, Contr. U.S. Natl. Herb. 25: 546. 1925, based on *Bigelovia menziesii* var. *scopulorum* M. E. Jones, Proc. Calif. Acad. Sci. II, 5: 692. 1895.

TYPE: Near Cedar City, Iron Co., Utah, 6,000 feet, 10 May 1894, *M. E. Jones 5204v* is the first of two collections cited (POM).

STATUS: Uncommon, habitat specific,

neither endangered nor threatened (Ripley, T).

Distribution: Iron, Kane (?), and San Juan (*Welsh & Moore 2447; Welsh 8813; Atwood 4100* [bry]) counties, Utah, and Coconino Co., Arizona (McDougall 1973).

Helianthus anomalus Blake, J. Wash. Acad. Sci. 21: 333. 1931.

Type: Desert between Hanksville and Henry Mts., Wayne Co., Utah, 5 Jul 1930, *Stanton 4806* (us).

Status: Restricted to dunes and sandy washes, where locally abundant, neither threatened nor endangered.

Distribution: Emery, Garfield, Grand, Juab, Kane, Millard, San Juan, Tooele, Uintah, Washington, and Wayne counties, Utah, and northern Arizona (Blauer 1966).

Helianthus canus (Britton) Wooton & Standley, Contr. U.S. Natl. Herb. 6: 190. 1913, based on *Helianthus petiolaris* var. *canus* Britton. Mem. Torrey Bot. Club 5: 334. 1894.

Status: Rare, possibly threatened.

Distribution: San Juan Co., Utah (*Cottam 2544* [bry]), and from western Texas to southern California and northern Mexico.

Helianthus deserticolus Heiser, Proc. Indiana Acad. Sci. 70: 209. 1961.

Type: 3.3 miles west of Hurricane, Washington Co., Utah, 29 Jun 1957, *Stoutamire 2574* (ind).

Status: Rare, restricted and possibly threatened.

Distribution: Washington Co., Utah, Mohave Co., Arizona, and Clark Co., Nevada (Heiser 1961).

Heterotheca jonesii (Blake) Welsh & Atwood, comb. nov., based on *Chrysopsis jonesii* Blake in Tidestrom, Contr. U.S. Natl. Herb. 25: 536. 1925, a substitute name for *C. caespitosa* M. E. Jones, Proc. Calif. Acad. Sci. II, 5: 694. 1895, not Nutt.

Type: Springdale, Washington Co., Utah, 4,000 feet, 16 May 1894, *M. E. Jones 5249u* (pom).

Status: Endemic, rare, local, and endangered.

Distribution: Washington and Garfield (*Harrison 12343* [bry]) counties, Utah.

Heterotheca grandiflora Nutt., Trans. Amer. Philos. Soc. II, 7: 315. 1840.

Status: Rare, local and restricted.

Distribution: Washington Co., Utah (*Welsh et al. 9530* [bry]); also in California and Arizona.

Heterotheca subaxillaris Britton & Rusby, Trans. New York Acad. Sci. 7: 10. 1887.

Status: Rare, possibly endangered.

Distribution: Grand Co., Utah (*Welsh & Moore 2744* [bry]); widespread elsewhere in the United States.

Hulsea heterochroma A. Gray, Proc. Amer. Acad. Arts 7: 359. 1868.

Status: Local, rare and possibly threatened.

Distribution: Washington Co., Utah (*Higgins & Atwood 1410* [bry]; Higgins 1972b); California and southern Nevada.

Hymenopappus filifolius Hook. var. *alpestris* (Maguire) Shinners, Rhodora 61: 155. 1959, based on *H. nudipes* var. *alpestris* Maguire, Amer. Midl. Naturalist 37: 144. 1947 (includes var. *nudipes* (Maguire) Turner).

Type: Cedar Breaks rim, Iron Co., Utah, 23 Jun 1940, *Maguire 19023* (ny).

Status: Restricted but locally common, not threatened nor endangered.

Distribution: Duchesne, Garfield, Iron, Kane, Piute, Sevier, Summit, and Utah counties, Utah, and Lincoln Co., Wyoming (Turner 1956).

Hymenopappus filifolius Hook. var. *tomentosus* (Rydb.) Turner, Rhodora 58: 237. 1956, based on *H. tomentosus* Rydb., Bull. Torrey Bot. Club 27: 633. 1900.

Type: St. George, Washington Co., Utah, 1877, *Palmer 270* (ny).

Status: Endemic, rare and restricted, threatened (Ripley, T).

Distribution: Kane and Washington counties, Utah (Turner 1956).

Hymenoxys depressa (Torr. & Gray ex Gray) Welsh & Reveal, comb. nov., based on *Actinella depressa* Torr. & Gray ex Gray, Mem. Amer. Acad. Arts II, 4: 100. 1849.

Status: Rare and local, possibly threatened.

Distribution: Emery (bry) and

Garfield (UT) counties, Utah, and from Colorado.

Lepidospartum latisquamum S. Wats., Proc. Amer. Acad. Arts 25: 133. 1890.

STATUS: Restricted and rare, possibly threatened.

DISTRIBUTION: Millard Co., Utah (BRY), and adjacent Nevada west to eastern California.

Lygodesmia grandiflora (Nutt.) Torr. & Gray var. *stricta* Maguire, Amer. Midl. Naturalist 37: 145. 1947.

TYPE: Frequent on adobe clay, 1 mile south of Price, Carbon Co., Utah, 5 Jun 1940, *Maguire 18417* (NY).

STATUS: Endemic, rare, restricted and endangered.

DISTRIBUTION: Carbon Co., Utah; known only from the type locality.

Machaeranthera glabriuscula (Nutt.) Cronq. & Keck var. *confertifolia* Cronq., Leafl. W. Bot. 10: 11. 1963.

TYPE: Barren clay slopes in pinyon-juniper zone, 11 miles northeast of Henrieville, Garfield Co., Utah, 7,000 feet, 31 May 1961, *Cronquist 9164* (NY).

STATUS: Endemic, rare and threatened.

DISTRIBUTION: Garfield and Kane counties, Utah (BRY, UTC).

Machaeranthera grindelioides (Nutt.) Shinners var. *depressa* (Maguire) Cronq. & Keck, Brittonia 9: 237. 1957, based on *Haplopappus nuttallii* var. *depressa* Maguire, Amer. Midl. Naturalist 37: 144. 1947.

TYPE: Warm Point, 5 miles southwest of Desert Range Experiment Station headquarters, Millard Co., Utah, 10 Jun 1941, *Maguire 20859* (NY).

STATUS: Rare and restricted, neither threatened nor endangered (Ripley, T).

DISTRIBUTION: Beaver and Millard counties, Utah (BRY), and Eureka, Lincoln and White Pine counties, Nevada (Maguire 1947).

Machaeranthera kingii (D. C. Eaton) Cronq. & Keck, Brittonia 9: 238. 1957, based on *Aster kingii* D. C. Eaton in King, Rep. Geol. Explor. 40th Parallel 5: 141. 1871.

TYPE: Wasatch Mts., above Cottonwood Canyon, Salt Lake Co., Utah, 1869, 9,000 feet, *Watson 507* (GH).

STATUS: Endemic, rare and restricted, possibly threatened.

DISTRIBUTION: Cache, Salt Lake and Utah counties, Utah (BRY, UTC).

Malacothrix clevelandii A. Gray, Bot. Calif. 1: 433. 1876.

STATUS: Local and infrequent.

DISTRIBUTION: Washington Co., Utah (*Atwood 4966* [BRY, WTS]); also in Nevada and California.

Parthenium ligulatum (M. E. Jones) Barneby, Leafl. W. Bot. 5: 20. 1947, based on *P. alpinum* var. *ligulatum* M. E. Jones, Contr. W. Bot. 13: 16. 1910.

TYPE: On nearly bare clayey and gravelly knolls on ridges, Theodore [now Duchesne], Duchesne Co., Utah, 6,000 feet, *M. E. Jones s.n.* (POM).

STATUS: Endemic, rare and restricted, threatened (Ripley, T).

DISTRIBUTION: Duchesne and Emery counties, Utah (BRY, NY).

Senecio dimorphophyllus Greene var. *intermedius* Barkley, Trans. Kansas Acad. Sci. 65: 363. 1962.

TYPE: Edge of swampy places, Geyser Pass, LaSal Mts. Utah, 10,500 feet, *Payson & Payson 4097* (MO).

STATUS: Endemic, rare, restricted and threatened (Ripley, T).

DISTRIBUTION: San Juan Co., Utah; known only from the type area.

Sphaeromeria capitata Nutt., Trans. Amer. Philos. Soc. II, 7: 402. 1841.

STATUS: Local and rare, threatened.

DISTRIBUTION: Grand Co., Utah (UTC); Wyoming and southern Montana.

Townsendia aprica Welsh & Reveal, Brittonia 20: 375. 1968.

TYPE: Ca 6 miles south of Fremont Junction along Utah Highway 72, on low, rolling exposed gray clay slopes, among scattered igneous boulders, Sevier Co., Utah, ca 6,500 feet, 1 May 1966, *Reveal & Welsh 721* (BRY).

STATUS: Endemic, rare and restricted, endangered (Ripley, E).

DISTRIBUTION: Sevier Co., Utah (BRY; Welsh & Reveal 1968).

Townsendia mensana M. E. Jones, Contr. W. Bot. 13: 15. 1910.

Type: Benches of the Uinta Mts., near Theodore [now Duchesne], Duchesne Co., Utah, 14 May 1908, *M. E. Jones s.n.* (POM).

Status: Endemic, locally restricted, possibly threatened.

Distribution: Duchesne and Uintah counties, Utah (Reveal 1970b).

Townsendia minima Eastw., Leafl. W. Bot. 1: 206. 1936.

Type: Bryce Canyon, Garfield Co., Utah, 19 Jun 1933, *Eastwood & Howell 727* (CAS).

Status: Endemic, edaphically restricted, possibly threatened.

Distribution: Garfield and Kane counties, Utah (Beaman 1957; Reveal 1970b).

Viguiera soliceps Barneby, Leafl. W. Bot. 10: 316. 1966.

Type: Locally plentiful on gumbo-clay knolls and bluffs, lower Cottonwood Canyon near its confluence with Paria River, about 41 miles southeast of Cannonville, Kane Co., Utah, 4,500 feet, 12 Jun 1966, *Barneby 14435* (NY).

Status: Endemic, local on Tropic Shale formation, threatened (Ripley, E).

Distribution: Cottonwood Canyon east to Last Chance Canyon, Kane Co., Utah (BRY, UTC).

Xanthocephalum sarothrae (Pursh) Shinners var. *pomariense* (Welsh) Welsh, comb. nov., based on *Gutierrezia sarothrae* (Pursh) Britton & Rusby var. *pomariensis* Welsh, Great Basin Nat. 30: 19. 1970.

Type: Sandy flat, base of sandstone cliffs, Frontier formation, mouth of Orchard Creek Draw, Dinosaur N.M., Uintah Co., Utah, 2 Oct 1969, *Welsh et al. 9471* (BRY).

Status: Endemic, rare and threatened.

Distribution: Uintah Co., Utah (Welsh 1970b).

Berberidaceae

Berberis fendleri A. Gray, Mem. Amer. Acad. Arts II, 4: 5. 1849.

Status: Rare, floristically restricted to seeps and hanging gardens.

Distribution: San Juan (*Maguire 5904, Holmgren 13850* [UTC]; *Moore 204a; Welsh & Moore 3839* [BRY]; Maguire 1937); southern Colorado and New Mexico.

Betulaceae

Betula x utahensis Britton, Bull. Torrey Bot. Club 31: 165. 1904.

Type: City Creek Canyon, Salt Lake Co., Utah, 18 Apr 1900, *Stokes s.n.* (NY).

Status: Rare; a putative hybrid between *B. occidentalis* Hook and *B. papyrifera* Marsh.

Distribution: In Utah known only from the type locality; the hybrid is widespread north of Utah (Dugle 1966).

Ostrya knowltonii Coville, Gard. & Forest 7: 114. 1894.

Status: Rare, disjunct in hanging gardens, along seeps and on slickrock in sandstone canyons.

Distribution: Grand (*Cottam 2145* and *556* [BRY, UTC]), Kane (*Welsh & Toft 11871* [BRY]), San Juan (*Welsh et al. 2939, 2961* and *3721; Moore 336; Welsh 11893; Welsh & Moore 11783; Welsh & Atwood 11693* and *11711; Atwood 4103* [BRY]); northern Arizona, southwestern New Mexico and western Texas (Little 1953; Correll & Johnston 1970).

Boraginaceae

Cryptantha barnebyi I. M. Johnston, J. Arnold Arbor. 29: 240. 1948.

Type: Ca 30 miles south of Ouray on white shale knolls, Uintah Co., Utah, 17 Jun 1947, *Ripley & Barneby 8748* (GH).

Status: Endemic, rare, threatened (Ripley, T).

Distribution: Uintah Co., Utah (Higgins 1971).

Cryptantha breviflora (Osterh.) Payson, Ann. Missouri Bot. Gard. 14: 318. 1927, based on *Oreocarya breviflora* Osterh. ex Payson, Univ. Wyoming Publ. Sci., Bot. 1: 169. 1926.

Type: 6.5 miles north of Jensen, Uintah Co., Utah, 19 Jun 1925, *Osterhout 6414* (RM).

Status: Endemic, locally common in the Uinta Basin, neither threatened nor endangered (Ripley, E).

DISTRIBUTION: Daggett, Duchesne and Uintah counties, Utah (Higgins 1971).

Cryptantha capitata (Eastw.) I. M. Johnston, J. Arnold Arbor. 21: 66. 1941, based on *Oreocarya capitata* Eastw., Leafl. W. Bot. 1: 9. 1937.

STATUS: Rare and obscure.

DISTRIBUTION: Garfield, Kane, Washington, and Wayne counties, Utah (Higgins 1971), and in Coconino Co., Arizona.

Cryptantha compacta Higgins, Great Basin Nat. 28: 196. 1968.

TYPE: Ca 8 miles west of Desert Range Experiment Station headquarters, along Utah Highway 21, Millard Co., Utah, 18 Jun 1968, *Higgins 1613* (BRY).

STATUS: Endemic, rare and local, threatened (Ripley, T).

DISTRIBUTION: Millard Co., Utah (Higgins 1971).

Cryptantha elata (Eastw.) Payson, Ann. Missouri Bot. Gard. 14: 285. 1927, based on *Oreocarya elata* Eastw., Bull. Torrey Bot. Club 30: 241. 1903.

STATUS: Rare and possibly threatened (Ripley, T).

DISTRIBUTION: Grand Co., Utah, and adjacent Mesa Co., Colorado (Higgins 1971).

Cryptantha grahamii I. M. Johnston, J. Arnold Arbor. 20: 391. 1939.

TYPE: On bench west of Green River, north of the mouth of Sand Wash, Uintah Co., Utah, 28 May 1933, *Graham 7924* (GH).

STATUS: Endemic, locally abundant, on white shale outcrops along Willow Creek, possibly threatened (Ripley, E).

DISTRIBUTION: Uintah Co., Utah (Higgins 1971).

Cryptantha johnstonii Higgins, Great Bain Nat. 28: 195. 1968.

TYPE: 15 miles west of U.S. Highway 50-6 along the road from Woodside to Castle Dale, Emery Co., Utah, 25 May 1968, *Higgins 1310* (BRY).

STATUS: Endemic, locally common, threatened (Ripley, E).

DISTRIBUTION: Emery Co., Utah (Higgins 1971).

Cryptantha jonesiana (Payson) Payson, Ann. Missouri Bot. Gard. 14: 323. 1927, based on *Oreocarya jonesiana* Payson, Univ. Wyoming Publ. Sci., Bot. 1: 168. 1926.

TYPE: San Rafael Swell, Emery Co., Utah, 15 May 1914, *M. E. Jones s.n.* (POM).

STATUS: Endemic, rare except in clay barrens in the San Rafael Swell, threatened (Ripley, E).

DISTRIBUTION: San Rafael Swell, Emery Co., Utah (Higgins 1971).

Cryptantha longiflora (A. Nels.) Payson, Ann. Missouri Bot. Gard. 14: 326. 1927, based on *Oreocarya loniflora* A. Nels., Erythea 7: 67. 1899.

STATUS: Rare and restricted in Grand Valley.

DISTRIBUTION: Grand Co., Utah, and west central Colorado (Higgins 1971).

Cryptantha mensana (M. E. Jones) Payson, Ann. Missouri Bot. Gard. 14: 333. 1927, based on *Krynitzkia mensana* M. E. Jones, Contr. W. Bot. 13: 14. 1910.

TYPE: Emery, Emery Co., Utah, 16 May 1894, *M. E. Jones 5445p* (POM).

STATUS: Rare and restricted to clay soils; threatened.

DISTRIBUTION: Carbon, Emery, and Grand counties, Utah (Higgins 1971).

Cryptantha ochroleuca Higgins, Great Basin Nat. 28: 197. 1968.

TYPE: On an outcrop 100 meters south of Red Canyon Campground, along Utah Highway 12, 21 Jul 1968, *Higgins 1788* (BRY).

STATUS: Endemic, rare and endangered (Ripley, E).

DISTRIBUTION: Garfield Co., Utah (Higgins 1971) .

Cryptantha osterhoutii (Payson) Payson, Ann. Missouri Bot. Gard. 14: 329. 1927, based on *Oreocarya osterhoutii* Payson, Univ. Wyoming Publ. Sci., Bot. 1: 167. 1926.

STATUS: Rare or obscure.

DISTRIBUTION: Disjunct in Duchesne, San Juan, and Wayne counties, Utah, and in Mesa Co., Colorado (Higgins 1971).

Cryptantha paradoxa (A. Nels.) Payson, Ann. Missouri Bot. Gard. 14: 330.

1927, based on *Oreocarya paradoxa* A. Nels., Bot. Gaz. 56: 69. 1913.

STATUS: Rare, San Rafael Swell, threatened.

DISTRIBUTION: Emery Co., Utah, western Colorado and northwestern New Mexico (Higgins 1971).

Cryptantha rollinsii I. M. Johnston, J. Arnold Arbor. 20: 391. 1939.

TYPE: Shale hillside on Thorne's Ranch, near Willow Creek, ca 22 miles south of Ouray, Uintah Co., Utah, 16 Jun 1937, *Rollins 1715* (GH).

STATUS: Endemic, locally common, neither threatened nor endangered.

DISTRIBUTION: Uinta Basin, in both Duchesne and Uintah counties, and on the San Rafael Swell, Emery Co., Utah (Higgins 1971).

Cryptantha semiglabra Barneby. Leafl. W. Bot. 3: 197. 1943.

STATUS: Rare and restricted, threatened (Ripley, T).

DISTRIBUTION: Vicinity of Fredonia, Coconino, and Mohave counties, Arizona, and in Washington Co., Utah (Higgins 1971).

Cryptantha stricta (Osterh.) Payson, Ann. Missouri Bot. Gard. 14: 264. 1927, based on *Oreocarya stricta* Osterh., Bull. Torrey Bot. Club 50: 217. 1923.

STATUS: Rare, but neither threatened nor endangered (Ripley, T).

DISTRIBUTION: Daggett, Summit, and Uintah counties, Utah; also in Moffat Co., Colorado, and Carbon Co., Wyoming (Higgins 1971).

Cryptantha tenuis (Eastw.) Payson, Ann. Missouri Bot. Gard. 14: 327. 1927, based on *Oreocarya tenuis* Eastw., Bull. Torrey Bot. Club 30: 244. 1903.

TYPE: Court House Wash, near Moab, Grand Co., Utah, 25 May 1892, *Eastwood s.n.* (CAS).

STATUS: Endemic, common and widespread.

DISTRIBUTION: Emery, Grand, San Juan, and eastern Wayne counties, Utah (Higgins 1971).

Cryptantha wetherillii (Eastw.) Payson, Ann. Missouri Bot. Gard. 14: 324. 1927, based on *Oreocarya wetherillii* Eastw., Bull. Torrey Bot. Club 30: 242. 1930.

TYPE: Court House Wash, near Moab, Grand Co., Utah, 25 May 1892, *Eastwood s.n.* (CAS).

STATUS: Endemic, common and widespread.

DISTRIBUTION: Carbon, Emery, Garfield, Grand, and Wayne counties, Utah (Higgins 1971).

Hackelia patens (Nutt.) I. M. Johnston var. *harrisonii* J. L. Gentry, Southw. Naturalist 19: 140. 1974.

TYPE: Pine Valley Mts., ca 1.5 miles up Forsyth Trail from Pine Valley, 30 May 1968, 7,300 feet, *Gentry 2002* (NY).

STATUS: Endemic, restricted but locally common.

DISTRIBUTION: Utah, Wasatch, and Washington counties, Utah (Gentry 1974).

Mertensia arizonica Greene, Pittonia 3: 197. 1897.

TYPE: "Arizona," without definite locality, but more likely from southern Utah, 1869, *Palmer s.n.* (US).

STATUS: Endemic (?), locally common; the var. *arizonica* is not known from Arizona in modern times.

DISTRIBUTION: Beaver, Garfield, Iron, Piute, and Washington counties, Utah (Higgins 1972a).

Mertensia viridis A. Nels. var. *cana* (Rydb.) L. O. Williams, Ann. Missouri Bot. Gard. 24: 115. 1937, based on *M. cana* Rydb., Bull. Torrey Bot. Club 36: 698. 1909.

STATUS: Rare and restricted, possibly threatened.

DISTRIBUTION: Bald Mtn., Summit Co., Utah (*Maguire 14699; Weber 3894* [UTC]) and north central Colorado (Williams 1937; Higgins 1972a).

Mertensia viridis A. Nels. var. *dilatata* (A. Nels.) L. O. Williams, Ann Missouri Bot. Gard. 24: 113. 1937, based on *M. coriacea* var. *dilatata* A. Nels., Bull. Torrey Bot. Club 29: 403. 1902.

STATUS: Rare, known from a single collection from the Uinta Mts.

DISTRIBUTION: Daggett Co., Utah (*Williams 599* [RM]); southeastern Wyoming and adjacent Colorado (Williams 1937; Higgins 1972a).

BRASSICACEAE

Arabis demissa Greene var. *languida* Rollins, Rhodora 43: 388. 1941.

STATUS: Rare and possibly threatened (Ripley, T).

DISTRIBUTION: Daggett Co., Utah (Rollins 1941); Albany and Sweetwater counties, Wyoming.

Arabis demissa Greene var. *russeola* Rollins, Rhodora 43: 387. 1941.

TYPE: Ca 18 miles north of Vernal, Uintah Co., Utah, Jun 1937, *Rollins 1757* (GH).

STATUS: Rare and threatened (Ripley, T).

DISTRIBUTION: Daggett and Uintah counties, Utah, and Albany Co., Wyoming (Rollins 1941).

Caulanthus divaricatus Rollins, Contr. Gray Herb. 201: 8. 1971.

TYPE: Ca 75 miles west of Blanding and 10 miles east of Hite, San Juan Co., Utah, 16 May 1961, *Cronquist 9033* (NY).

STATUS: Endemic, rare though widespread, neither threatened nor endangered.

DISTRIBUTION: Carbon, Emery, Garfield, Grand, San Juan, and Wayne counties, Utah (BRY, UTC).

Draba maguirei C. L. Hitchc., Univ. Wash. Publ. Biol. 11: 71. 1941.

TYPE: Rocky soil on east slope of Mt. Naomi, Bear River Range, Cache Co., Utah, 9,600 feet, *Maguire et al. 14161* (WTU).

STATUS: Endemic, restricted and possibly threatened.

DISTRIBUTION: Cache Co., Utah (Hitchcock 1941).

Draba maguirei C. L. Hitchc. var. *burkei* C. L. Hitchc., Univ. Wash. Publ. Biol. 11: 72. 1941.

TYPE: Cottonwood Canyon, Wellsville Mts., Box Elder Co., Utah, 25 May 1932, *Burke 2968* (UT).

STATUS: Endemic, restricted and threatened.

DISTRIBUTION: Box Elder (Hitchcock 1941) and Weber (*Clark 2332* [BRY, WSCO]) counties, Utah.

Draba pectinipila Rollins, Rhodora 55: 231. 1953.

STATUS: Endangered or possibly extirpated.

DISTRIBUTION: Flaming Gorge, Daggett Co., Utah, and adjacent Sweetwater Co., Wyoming (Rollins 1953).

Draba sobolifera Rydb., Bull. Torrey Bot. Club 30: 251. 1903.

TYPE: Marysvale, Piute Co., Utah, above timber line, 1894, *M. E. Jones 5936* (US).

STATUS: Endemic, rare and threatened (Ripley, T).

DISTRIBUTION: Garfield and Piute counties, Utah (Hitchcock 1941).

Draba subalpina Goodman & Hitchc., Ann. Missouri Bot. Gard. 19: 77. 1932.

TYPE: Cedar Breaks, Iron Co., Utah, *Goodman & Hitchcock 1622* (MO).

STATUS: Endemic, infrequent and possibly threatened (Ripley, T).

DISTRIBUTION: Garfield, Iron and Kane counties, Utah (BRY, UTC).

Draba zionensis C. L. Hitchc., Univ. Wash. Publ. Biol. 11: 49. 1941.

TYPE: Zion Canyon, Washington Co., Utah, 7 May 1923, *M. E. Jones s.n.* (POM).

STATUS: Endemic, rare and threatened (Ripley, T).

DISTRIBUTION: Juab (Cottam 7201 UT) and Washington counties, Utah (Hitchcock 1941).

Glaucocarpum suffrutescens (Rollins) Rollins, Madroño 4: 233. 1938, based on *Thelypodium suffrutescens* Rollins in Graham, Ann. Carnegie Mus. 26: 244. 1937.

TYPE: West of Willow Creek, on Thorne's Ranch, eastern slope of Big Pack Mtn., Uintah Co., Utah, 23 May 1935, *Graham 8950* (GH).

STATUS: Endemic, rare and endangered (Ripley, E).

DISTRIBUTION: Uintah Co., Utah; known only from the type locality (Rollins 1938).

Lepidium barnebyanum Reveal, Great Basin Nat. 27: 178. 1967, based on *L. montanum* Nutt. ex Torr. & Gray ssp. *demissum* C. L. Hitchc., Madroño 10: 157. 1950.

TYPE: Indian Creek Canyon, on white shale ridge tops, ca 4 miles southwest of Duchesne, Duchesne Co., Utah, 15 Jun 1947, *Ripley & Barneby 8699* (WTU).

STATUS: Endemic, rare and endangered (Ripley, E).

DISTRIBUTION: Duchesne Co., Utah; known only from the type locality (Reveal 1967).

Lesquerella garrettii Payson, Ann. Missouri Bot. Gard. 8: 213. 1921.

TYPE: Big Cottonwood Canyon, Salt Lake Co., Utah, 28 Jun 1908, *Garrett 1344* (MO).

STATUS: Endemic, rare and possibly threatened (Ripley, T).

DISTRIBUTION: Salt Lake, Utah and Wasatch counties, Utah (Rollins & Shaw 1973).

Lesquerella hemiphysaria Maguire, Amer. Midl. Naturalist 27: 456. 1942.

TYPE: Frequent, limestone breaks, south side of Middle Fork Park, Wasatch Plateau, 10 Aug 1940, 10,800 feet, *Maguire 20053* (UTC).

STATUS: Endemic, locally common but restricted.

DISTRIBUTION: Carbon, Emery, Sanpete, and Utah counties, Utah (Rollins & Shaw 1973).

Lesquerella rubicundula Rollins, Contr. Dudley Herb. 3: 178. 1941.

TYPE: Red Canyon, Garfield Co., Utah, 2,300 meters, 6 Jul 1912, *Eggleston 8198* (NA, the type now transferred to US).

STATUS: Endemic, rare and threatened (Ripley, T).

DISTRIBUTION: Garfield, Kane, and Piute counties, Utah (Reveal 1970a; Rollins & Shaw 1973).

Lesquerella tumulosa (Barneby) Reveal, Great Basin Nat. 30: 97. 1970, based on *L. hitchcockii* Munz ssp. *tumulosa* Barneby, Leafl. W. Bot. 10: 313. 1966.

TYPE: Bare white shale knolls, 6.5 miles southeast of Cannonville, Kane Co., Utah, 12 Jun 1966, *Barneby 14424* (NY).

STATUS: Endemic, rare and endangered.

DISTRIBUTION: Kane Co., Utah; known only from the type locality (Reveal 1970a).

Lesquerella utahensis Rydb., Bull. Torrey Bot. Club 30: 252. 1903.

TYPE: American Fork Canyon, Utah Co., Utah, 31 Jul 1880, *M. E. Jones 1354* (NY).

STATUS: Endemic, rare to locally common.

DISTRIBUTION: Davis, Duchesne, Juab, Salt Lake, Summit, Tooele, Uintah, Utah, Wasatch and Weber counties, Utah (Rollins & Shaw 1973).

Parrya rydbergii Botsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 17: 178. 1955, based on *P. platycarpa* Rydb., Bull. Torrey Bot. Club 39: 326. 1912, not Hook. f. & Thomas.

TYPE: Uinta Mts., Aug 1869, *Watson 54* (NY).

STATUS: Endemic, rare and threatened (Ripley, T).

DISTRIBUTION: Crest of the Uinta Mts., Duchesne (*Murdock 54* [BRY]) and Daggett-Uintah counties (*Waite 252* and *297* [BRY]).

Physaria grahamii Morton in Graham, Ann. Carnegie Mus. 26: 220. 1937.

TYPE: Chandler Canyon, Uintah Co., Utah, 3 Aug 1935, 6,000 feet, *Graham 9976* (US).

STATUS: Endemic, rare and possibly extinct (Ripley, PoEx).

DISTRIBUTION: Uintah Co., Utah; known only from the type collection as recent efforts to recollect this species have failed (Waite 1973).

Thelypodium integrifolium (Nutt.) Endl. var. *complanatum* (Al-Shehbaz) Welsh & Reveal, stat. nov., based on *T. integrifolium* ssp. *complanatum* Al-Shehbaz, Contr. Gray Herb. 204: 105. 1973.

STATUS: Local and infrequent.

DISTRIBUTION: Box Elder Co., Utah (UTC; Al-Shehbaz 1973); found to the west of Utah.

Thelypodium rollinsii Al-Shehbaz, Contr. Gray Herb. 204: 97. 1973.

TYPE: On alkaline soil in the vicinity of the Sevier River, ca 12 miles north of Scipio along U.S. Highway 91, 29 Jul 1969, *Al-Shehbaz & Al-Shehbaz 6913* (GH).

STATUS: Endemic, locally common, neither threatened nor endangered.

DISTRIBUTION: Carbon, Juab, Millard, Piute, Sanpete, and Sevier counties, Utah (Al-Shehbaz 1973).

Thelypodium sagittatum (Nutt.) Endl. ex Walp. var. *ovalifolium* (Rydb.) Welsh & Reveal, stat. & comb. nov., based on *T. ovalifolium* Rydb., Bull. Torrey Bot. Club 30: 253. 1903.

Type: Panguitch Lake, Garfield Co., Utah, 7 Sep 1894, *M. E. Jones 6015e* (us).

Status: Rare and restricted, possibly threatened.

Distribution: Garfield and Iron counties, Utah, and White Pine Co., Nevada (Al-Shehbaz 1973).

Cactaceae

Echinocereus engelmannii (Parry) Lemaire var. *purpureus* L. Benson, Cact. Succ. J. (Los Angeles) 41: 127. 1969.

Type: Mojavean desert north of St. George, Washington Co., Utah, 5 May 1949, 2,900 feet, *Benson 13637* (pom).

Status: Endemic, rare and endangered (Ripley, E).

Distribution: Washington Co., Utah; known only from the vicinity of the type locality (Benson 1969b).

Ferocactus acanthodes (Lemaire) Britton & Rose, Publ. Carnegie Inst. Wash. 248 (3): 129. 1922, based on *Echinocactus acanthodes* Lemaire, Cact. Gen. Nov. Sp. 106. 1839.

Status: Restricted and endangered.

Distribution: Washington Co., Utah (bry); southern Nevada, Arizona and California (Benson 1969b).

Mammillaria tetrancistra Engelm., Amer. J. Sci. Arts II, 14: 337. 1852.

Status: Restricted and rare, possibly threatened.

Distribution: Washington Co., Utah; southern Nevada, California, and Arizona (Benson 1969b).

Opuntia pulchella Engelm., Trans. Acad. Sci. St. Louis 2: 201. 1863.

Status: Rare, restricted and possibly threatened.

Distribution: Millard Co., Utah (bry); Nevada and Arizona (Benson 1957). This species includes those entities included in *Micropuntia* by Daston (1946).

Opuntia whipplei Engelm. & Bigelow var. *multigeniculata* L. Benson, Cact. Ariz. ed. 3, 38. 1969.

Status: Restricted and rare.

Distribution: Washington Co., Utah, and adjacent Nevada and Arizona (Benson 1969b).

Pediocactus sileri (Engelm.) L. Benson, Cact. Succ. J. (Los Angeles) 33: 53. 1961, based on *Echinocactus sileri* Engelm. ex Coulter, Contr. U.S. Natl. Herb. 3: 376. 1896.

Type: Cottonwood Springs and Pipe Springs, supposedly from southern Utah but more likely from Arizona, 1883, *Siler s.n.* (mo).

Status: Arizona Strip endemic, rare, local and endangered (Ripley, E).

Distribution: Washington Co., Utah (*Welsh 12712* [bry]), and northern Arizona (bry; Benson 1969b).

Sclerocactus glaucus (K. Schum.) L. Benson, Cact. Succ. J. (Los Angeles) 38: 53. 1966, based on *Echinocactus glaucus* K. Schum., Gessammtb. Kakt. 438. 1898.

Status: Rare, possibly extirpated from Utah (Ripley, E).

Distribution: Duchesne and Uintah counties, Utah, and Delta Co., Colorado (Benson 1966).

Sclerocactus pubispinus (Engelm.) L. Benson, Cact. Succ. J. (Los Angeles) 38: 103. 1966, based on *Echinocactus pubispinus* Engelm., Trans. Acad. Sci. St. Louis 2: 199. 1863.

Status: Rare and threatened (Ripley, T).

Distribution: Box Elder, Beaver, and Sevier counties, Utah, and Elko Co., Nevada (Benson 1966).

Sclerocactus pubispinus (Engelm.) L. Benson var. *sileri* L. Benson, Cact. Ariz. ed. 3, 23. 1969.

Type: Southern Utah, 1888, *Siler s.n.* (ph).

Status: Rare and now extirpated from Utah.

Distribution: Kane Co., Utah, and Coconino Co., Arizona (Benson 1969b).

Sclerocactus whipplei (Engelm. & Bigelow) Britton & Rose var. *spinosior* (Engelm.) Boissev. in Boissev. & Davidson, Colorado Cacti 51. 1940, based on *Echinocactus whipplei* var. *spinosior* Engelm., Trans. Acad. Sci. St. Louis 2: 199. 1863.

TYPE: South of the Great Salt Lake Desert, 19 Jul 1859, *H. Engelmann s.n.* (MO).

STATUS: Rare to locally common, neither threatened nor endangered. (Ripley, T).[4]

DISTRIBUTION: Widespread in much of the southern two-thirds of Utah.

Sclerocactus wrightiae L. Benson, Cact. Succ. J. (Los Angeles) 38: 55. 1966.

TYPE: Near San Rafael Ridge, Emery Co., Utah, 5,000 feet, *Benson & Benson 16595* (POM).

STATUS: Endemic, restricted and rare, endangered (Ripley, T).

DISTRIBUTION: Emery and Wayne counties, Utah.

CAPPARIDACEAE

Cleomella palmerana M. E. Jones, Zoe 2: 236. 1891.

TYPE: Green River, Emery Co., Utah, 9 May 1890, *M. E. Jones s.n.* (POM).

STATUS: Endemic to the Navajo Basin of Utah and Colorado, edaphically restricted but neither threatened nor endangered.

DISTRIBUTION: Duchesne, Emery, Garfield, Grand, Kane, and Wayne counties, Utah (BRY), and Colorado (Harrington 1954).

Cleomella placosperma S. Wats. in King, Rep. Geol. Explor. 40th Parallel 5: 33. 1871.

STATUS: Restricted and rare, possibly threatened.

DISTRIBUTION: Iron Co., Utah (BRY), and Nevada (Shaw 1970).

CARYOPHYLLACEAE

Arenaria kingii (S. Wats.) M. E. Jones var. *plateauensis* (Maguire) Reveal, stat. nov., based on *A. kingii* ssp. *plateauensis* Maguire, Bull. Torrey Bot. Club 74: 54. 1947.

TYPE: Cedar Breaks Rim, Iron Co., Utah, 23 Jun 1940, 10,400 feet, *Maguire 19024* (UTC).

STATUS: Endemic, locally common, neither threatened nor endangered.

DISTRIBUTION: Beaver, Garfield, Kane, Iron, and Wayne counties, Utah (Maguire 1947b).

Silene petersonii Maguire, Madroño 6: 24. 1941.

TYPE: Skyline Drive, 1 mile above Baldy Ranger Station, Sanpete Co., Utah, 8 Aug 1940, 10,900 feet, *Maguire 20000* (UTC).

STATUS: Endemic, locally common but possibly threatened (Ripley, T).

DISTRIBUTION: Iron, Garfield and Sanpete counties, Utah (Maguire 1941; Hitchcock & Maguire 1951).

Silene petersonii Maguire var. *minor* Hitchc. & Maguire, Univ. Wash. Publ. Biol. 13: 38. 1947.

TYPE: Red Canyon, 5 miles east of U.S. Highway 89, Garfield Co., Utah, 16 Jul 1940, *Maguire 19550* (UTC).

STATUS: Endemic, rare and threatened.

DISTRIBUTION: Garfield Co., Utah; known only from the type area.

CHENOPODIACEAE

Atriplex bonnevillensis C. A. Hanson, Stud. Syst. Bot. 1: 2. 1962.

TYPE: Dry lake bed 1.5 miles northeast of Desert Range Experiment Station headquarters, Millard Co., 12 Jul 1961, *Hanson 354* (BRY).

STATUS: Restricted, though locally abundant, possibly threatened.

DISTRIBUTION: Juab and Millard counties, Utah (BRY), and Nevada (Hanson 1962b).

Atriplex garrettii Rydb., Bull. Torrey Bot. Club 39: 312. 1912.

TYPE: Vicinity of Moab, Grand Co., Utah, 1 Jul 1911, *Rydberg & Garrett 8465* (NY).

STATUS: Colorado River drainage, endemic, restricted but locally common.

DISTRIBUTION: Garfield, Grand, Kane, and San Juan counties, Utah (BRY), and reported from Colorado (Harrington 1954).

Atriplex obovata Moq., Chenop. Enum. 61. 1840.

STATUS: Restricted, rare and possibly threatened.

DISTRIBUTION: San Juan Co., Utah;

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[4] Cited by Ripley (1975) as *S. spinosior*, without author; we can find no indication that such a combination has been made. According to Benson (1966), this name is a synonym of *S. pubispinus* (Engelm.) L. Benson var. *pubspinus*.

rather common in Arizona, New Mexico and Mexico (Hanson 1692b).

Atriplex welshii C. A. Hanson, Stud. Syst. Bot. 1: 1. 1962.

TYPE: 4 miles south of Cisco along Utah Highway 128, Grand Co., Utah, 5 Jul 1961, *Hanson 322* (BRY).

STATUS: Endemic, restricted and possibly threatened.

DISTRIBUTION: Carbon and Grand counties, Utah (BRY).

CUCURBITACEAE

Cucurbita foetidissima H.B.K., Nov. Gen. & Sp. 2: 123. 1817.

STATUS: Restricted, but locally common and often weedy, neither threatened nor endangered.

DISTRIBUTION: San Juan (*Welsh et al. 2992* [BRY]), and Washington (BRY) counties, Utah, and widespread elsewhere.

CUSCUTACEAE

Cuscuta warneri Yuncker, Brittonia 12: 38. 1960.

TYPE: Vicinity of Powell, 15 miles west of Fillmore, Millard Co., Utah, 10 Sep 1957, on *Phyla cuneifolia, Warner s.n.* (UTC).

STATUS: Endemic, possibly extinct (Ripley, PoEx).

DISTRIBUTION: Millard Co., Utah; known only from the type collection (Yuncker 1960, 1965).

CYPERACEAE

Carex curatorum Stacey, Leafl. W. Bot. 2: 213. 1937.

STATUS: Rare and restricted to specialized habitats; threatened.

DISTRIBUTION: San Juan Co., Utah (*Welsh 12425* [BRY]), and in Grand Canyon, Arizona (Stacey 1937).

Cladium californicum (S. Wats.) O'Neill in Tidestr. & Kittell, Fl. Arizona & N. Mex. 773. 1941, based on *C. mariscus* var. *californicum* S. Wats., Bot. Calif. 2: 224. 1880.

STATUS: Rare, restricted and endangered.

DISTRIBUTION: Kane (*Welsh & Atwood 11709; Welsh & Moore 11780; Welsh & Toft 11870* [BRY]) and San Juan (*Welsh & Toft 11874* [BRY]), and from northern Arizona, southern Nevada, and southern California to Central America (Kearney & Peebles 1951).

ELAEAGNACEAE

Elaeagnus commutata Bernh., Allg. Thüring. Gartenzeitung 2: 137. 1843.

STATUS: Restricted, local and possibly extirpated from Utah.

DISTRIBUTION: Daggett (*Julander J56* [BRY]) and Summit (*Welsh & Moore 6724* [BRY]) counties, Utah; widespread northward to Alaska (Welsh 1974b).

ERICACEAE

Arctostaphylos pringlei Parry, Bull. Calif. Acad. Sci. 2: 494. 1887.

STATUS: Local, rare, possibly threatened.

DISTRIBUTION: Washington Co., Utah (*Higgins 665* and *3414* [BRY]; Higgins 1972b).

EUPHORBIACEAE

Euphorbia nephradenia Barneby, Leafl. W. Bot. 10: 314. 1966.

TYPE: Lower Cottonwood Canyon, about 41 miles southeast of Cannonville, Kane Co., Utah, 12 Jun 1966, 4,500 feet, *Barneby 14434* (NY).

STATUS: Endemic, restricted edaphically, threatened (Ripley, T).

DISTRIBUTION: Emery, Kane, and Wayne counties, Utah (BRY).

FABACEAE

Astragalus adanus A. Nels., Bot. Gaz. 53: 222. 1912.

STATUS: Rare and possibly extirpated from Utah.

DISTRIBUTION: Juab Co., Utah; widespread in Idaho (Barneby 1964).

Astragalus adsurgens Pallas ssp. *robustior* (Hook.) Welsh, Iowa State Coll. J. Sci. 37: 357. 1963, based on *A. adsurgens* var. *robustior* Hook., Fl. Boreali-Amer. 1: 149. 1831.

STATUS: Restricted, rare and possibly threatened.

DISTRIBUTION: Daggett Co., Utah (*Hanson 283a* [BRY]); widespread east of the continental divide northward to Alaska (Welsh 1974b).

Astragalus alpinus L., Sp. Pl. 760. 1753.
STATUS: Rare and local, possibly threatened.
DISTRIBUTION: Grand (*Holmgren et al. 2321* [BRY, NY, UTC]) and Salt Lake (UT, without collector) counties; widespread in North America and Eurasia (Welsh 1974b).

Astragalus ampullarius S. Wats., Amer. Naturalist 7: 300. 1873.
TYPE: Kanab, Kane Co., Utah, 1872, *Thompson s.n.* (GH).
STATUS: Arizona strip endemic, edaphically restricted and though locally common, probably threatened (Ripley, T).
DISTRIBUTION: Kane and Washington counties, Utah, and northernmost Coconino and Mohave counties, Arizona (BRY; Barneby 1964).

Astragalus asclepiadoides M. E. Jones, Zoe 2: 238. 1891.
TYPE: Cisco, Grand Co., Utah, 21 Jun 1889, *M. E. Jones s.n.* (POM)
STATUS: Edaphically restricted although locally common, neither threatened nor endangered.
DISTRIBUTION: Carbon, Duchesne, Emery, Garfield, Grand, Sanpete, Sevier (UT), Uintah, and Wayne counties, Utah (BRY, UTC), and western Colorado (Barneby 1964).

Astragalus australis Lam., Fl. Franç. 2: 637. 1778.
STATUS: Possibly extirpated from Utah.
DISTRIBUTION: Piute (?) Co., Utah (Barneby 1964).

Astragalus barneby Welsh & Atwood, nom. nov., based on *A. desperatus* M. E. Jones var. *conspectus* Barneby, Leafl. W. Bot. 5: 87. 1948.
STATUS: Rare, restricted and threatened (Ripley, T).
DISTRIBUTION: Garfield Co., Utah (BRY), and in Navajo and Coconino counties, Arizona (Barneby 1964).

This remarkable milkvetch is adequately distinct on account of size of flower and parts, and because of stature to segregate it from its near and mirror-imaged cogener *A. desperatus*. The name change honors the author of the monumental "Atlas of North American Astragalus," Rupert C. Barneby of the New York Botanical Garden.

Astragalus bodinii Sheldon, Minnesota Bot. Stud. 1: 122. 1894.
STATUS: Rare and endangered.
DISTRIBUTION: Wayne Co., Utah (BRY); widespread in Alaska, Canada, Colorado, Wyoming, and one record from Nebraska (Barneby 1964).

Astragalus brandegei Porter in Porter & Coulter, Syn. Fl. Colo. 24. 1872.
STATUS: Rare and obscure, probably threatened.
DISTRIBUTION: Carbon, Emery, Garfield, Piute, and Wayne counties, Utah (BRY); also in Colorado, New Mexico, and Arizona (Barneby 1964).

Astragalus bryantii Barneby, Proc. Calif. Acad. Sci. IV, 25: 156. 1944.
STATUS: Probably extirpated from Utah.
DISTRIBUTION: Kane Co., Utah, in Glen Canyon, the collection area inundated by Lake Powell; also in northern Arizona (Barneby 1964).

Astragalus callithrix Barneby, Leafl. W. Bot. 3: 102. 1942.
STATUS: Rare and restricted, possibly threatened (Ripley, T).
DISTRIBUTION: Millard Co., Utah (BRY); otherwise known only from two locations in Nye Co., Nevada.

Astragalus castaneiformis S. Wats. var. *consobrinus* Barneby, Amer. Midl. Naturalist 41: 496. 1949.
TYPE: Southeast of Bicknell, Wayne Co., Utah, 10 Jun 1947, 7,600 feet, *Ripley & Barneby 8605* (CAS).
STATUS: Endemic, rare and obscure, possibly threatened.
DISTRIBUTION: Garfield, Piute, Sevier, and Wayne counties, Utah (Barneby 1964).

Astragalus chloödes Barneby, Leafl. W. Bot. 5: 6. 1947.
TYPE: Ca 6 miles southeast of Jensen, Uintah Co., Utah, 7 Jun 1946, *Ripley & Barneby 7797* (CAS).
STATUS: Endemic, rare and threatened (Ripley, T).
DISTRIBUTION: Uintah Co., Utah (BRY, UTC).

Astragalus coltonii M. E. Jones, Zoe 2: 237. 1891.

TYPE: Canyons of the Coal Range east of Castle Gate, 27 Jun 1889, *M. E. Jones s.n.* (POM).

STATUS: Endemic, locally abundant, neither threatened nor endangered. Our plant is var. *coltonii*.

DISTRIBUTION: Carbon, Emery, Garfield, Kane, Sevier, and Wayne counties, Utah (BRY, UT, UTC).

Astragalus convallarius Greene var. *finitimus* Barneby, Leafl. W. Bot. 7: 192. 1954.

TYPE: Ca 3 miles south of Enterprise, Washington Co., Utah, 11 Jun 1942, *Ripley & Barneby 4767* (CAS).

STATUS: Rare and local, threatened (Ripley, T).

DISTRIBUTION: Washington Co., Utah, and adjacent Nevada (Barneby 1964).

Astragalus cottamii Welsh, Rhodora 72: 189. 1970.

TYPE: Ca 4 miles east of Clay Hills divide, San Juan Co., Utah, 1 May 1966, *Welsh 5207* (BRY).

STATUS: Restricted and local, possibly threatened (Ripley, T).

DISTRIBUTION: San Juan Co., Utah, and adjacent Monument Valley, Arizona (BRY).

Astragalus cronquistii Barneby, Mem. New York Bot. Gard. 13: 258. 1964.

TYPE: In desert along west side of Comb Wash, 9 miles west of Bluff, San Juan Co., Utah, 27 May 1961, *Cronquist 9123* (NY).

STATUS: Endemic and very restricted, endangered (Ripley, E).

DISTRIBUTION: San Juan Co., Utah (BRY, UTC).

Astragalus cymboides M. E. Jones, Proc. Calif. Acad. Sci. II, 5: 650. 1895.

TYPE: Huntington, Emery Co., Utah, 16 Jun 1894, at 5,000 feet, *M. E. Jones 5464j* (POM).

STATUS: Endemic, locally common to abundant, neither threatened nor endangered.

DISTRIBUTION: Carbon, Emery, Grand, and San Juan counties, Utah (BRY).

Astragalus deserticus Barneby, Mem. New York Bot. Gard. 13: 634. 1964.

TYPE: Common on slopes near Indianola, 17 Jun 1909, *Tidestrom 2249* (GH).

STATUS: Endemic and possibly extinct (Ripley, PrEx).

DISTRIBUTION: Sanpete Co., Utah (Barneby 1964).

Astragalus detritalis M. E. Jones, Contr. W. Bot. 13: 9. 1910.

TYPE: Ca 4 miles above Theodore [Duchesne] on the Colton road, Duchesne Co., Utah, 11 May 1908, *M. E. Jones s.n.* (POM).

STATUS: Uinta Basin endemic, local and possibly endangered (Ripley, E).

DISTRIBUTION: Duchesne and Uintah counties, Utah, and Rio Blanco Co., Colorado (BRY).

Astragalus diversifolius A. Gray, Proc. Amer. Acad. Arts 6: 230. 1864.

STATUS: Rare, disjunct and possibly extirpated from Utah.

DISTRIBUTION: Juab and Tooele counties; also in southern Idaho where rare (Barneby 1964).

Astragalus duchesnensis M. E. Jones, Contr. W. Bot. 13: 9. 1910.

TYPE: Ca 13 miles below Theodore [Duchesne] toward Chepeta Well, Duchesne Co., Utah, 23 May 1908, *M. E. Jones s.n.* (POM).

STATUS: Endemic, restricted and threatened (Ripley, T).

DISTRIBUTION: Duchesne and Uintah counties, Utah (BRY).

Astragalus eastwoodae M. E. Jones, Zoe 4: 368. 1894, based on *A. preussii* var. *sulcatus* M. E. Jones, Zoe 4: 37. 1893.

TYPE: Westwater, Grand Co., Utah (incorrectly given as "Colorado"), 6 May 1891, *M. E. Jones s.n.* (POM).

STATUS: Rare, disjunct and possibly threatened.

DISTRIBUTION: Emery, Grand, and San Juan counties, Utah; also in west central Colorado (Barneby 1964).

Astragalus emoryanus (Rydb.) Cory, Rhodora 38: 406. 1936, based on *Hamosa emoryana* Rydb., Bull. Torrey Bot. Club 54: 237. 1927.

STATUS: Rare and endangered.

DISTRIBUTION: Kane (*Atwood 4629* [BRY]) Co., Utah; Arizona, New Mexico, Texas, and Mexico (Barneby 1964).

Astragalus ensiformis M. E. Jones, Rev. Astrag. 226. 1923.

Status: Rare and local; threatened (Ripley, T).

Distribution: Washington Co., Utah, and Mohave Co., Arizona (bry).

Astragalus eucosmus B. L. Robinson, Rhodora 10: 33. 1908.

Status: Possibly extirpated.

Distribution: Summit Co., Utah; widespread in northern North America (Barneby 1964; Welsh 1974b).

Astragalus eurekensis M. E. Jones, Contr. W. Bot. 8: 12. 1898.

Type: Eureka, Juab Co., Utah, 1891, *M. E. Jones s.n.* (pom).

Status: Endemic, locally common to abundant, neither threatened nor endangered.

Distribution: Juab, Iron, Millard, Sanpete, Tooele, and Utah counties, Utah (bry; Barneby 1964).

Astragalus flavus Nutt. ex Torr. & Gray var. *argillosus* (M. E. Jones) Barneby, Mem. New York Bot. Gard. 13: 401. 1964, based on *A. argillosus* M. E. Jones, Zoe 2: 241. 1891.

Type: Green River, Emery Co., Utah, 7 May 1890, *M. E. Jones s.n.* (pom).

Status: Endemic, restricted edaphically but locally common, neither threatened nor endangered.

Distribution: Emery, Garfield, Grand, and Wayne counties, Utah (bry).

Astragalus gilviflorus Sheldon, Minnesota Bot. Stud. 1: 21. 1894, based on *A. triphyllus* Pursh, Fl. Amer. Sept. 2: 740. 1814, not Pallas.

Status: Rare or possibly extirpated from Utah.

Distribution: Summit Co., Utah (utc); widespread east of the continental divide (Barneby 1964).

Astragalus hallii A. Gray var. *fallax* (S. Wats.) Barneby, Leafl. W. Bot. 9: 91. 1960, based on *A. fallax* S. Wats., Proc. Amer. Acad. Arts 20: 362. 1885.

Status: Rare and local, possibly threatened.

Distribution: Garfield and Kane counties, Utah (bry).

Astragalus hamiltonii C. L. Porter, Rhodora 54: 159. 1952.

Type: On the Wasatch formation 5 miles south of Vernal, Uintah Co., Utah, 24 May 1950, *Hamilton & Beath s.n.* (rm).

Status: Endemic, rare and local, endangered (Ripley, E).

Distribution: Uintah Co., Utah (bry).

Astragalus harrisonii Barneby, Mem. New York Bot. Gard. 13: 271. 1964.

Type: Wash below the Natural Bridge, near Fruita, Wayne Co., Utah, 8 Jun 1961, *Barneby 13131* (cas).

Status: Endemic, rare and endangered (Ripley, E).

Distribution: Wayne Co., Utah; known only from the type area (bry).

Astragalus iodanthus S. Wats. in King, Rep. Geol. Explor. 40th Parallel 5: 70. 1871.

Status: Rare and possibly extirpated from Utah.

Distribution: Tooele Co., Utah; widespread to the west of Utah (Barneby 1964).

Astragalus iselyi Welsh, Great Basin Nat. 34: 305. 1974.

Type: Brumley Bridge, ca 1.5 miles north of Pack Creek Ranch, San Juan Co., Utah, 5 May 1971, *Welsh 10970* (bry).

Status: Endemic, edaphically restricted, endangered.

Distribution: Grand and San Juan counties, Utah (bry; Welsh 1974a).

Astragalus jejunus S. Wats. in King, Rep. Geol. Explor. 40th Parallel 5: 73. 1871.

Status: Rare and restricted, possibly threatened.

Distribution: Rich Co., Utah (Barneby 1964); southwestern Wyoming and in an isolated location in White Pine Co., Nevada.

Astragalus kentrophyta A. Gray var. *coloradoensis* M. E. Jones, Contr. W. Bot. 10: 63. 1902.

Status: Navajo Basin endemic; rare to locally common but probably threatened.

Distribution: Garfield, Kane, San Juan, and Wayne counties, Utah (bry), and adjacent northern Arizona (Barneby 1964).

Astragalus lancearius A. Gray, Proc. Amer. Acad. Arts 13: 370. 1878.

Status: Rare and local in generalized

habitats; possibly threatened (Ripley, T).

Distribution: Kane (BRY) and Washington counties, Utah and in Coconino and Mohave counties, Arizona (BRY; Barneby 1964).

Astragalus lentiginosus Dougl. ex Hook. var. *chartaceous* M. E. Jones, Proc. Calif. Acad. Sci. II, 5: 673. 1895.

Type: Ephraim, Sanpete Co., Utah, 13 Jul 1894, 6,000 feet, *M. E. Jones 5627m* (POM).

Status: Rare and local, possibly threatened (Ripley, PoEx, Tax?).[5]

Distribution: Daggett, Juab, Sanpete, Sevier, Summit, and Tooele counties, Utah, and widespread from Colorado, Wyoming, Idaho, Oregon, California, and Nevada (Schoener 1975).

Astragalus lentiginosus Dougl. ex Hook. var. *fremontii* (Gray ex Torr.) S. Wats. in King, Rep. Geol. Explor. 40th Parallel 5: 66. 1871, based on *A. fremontii* Gray ex Torr. in Whipple, Explor. & Surv. Railroad Route from Mississippi River to Pacific Ocean 4(5): 80. 1857.

Status: Rare and ephemeral, possibly threatened.

Distribution: Washington Co., Utah (BRY; Schoener 1974); widespread in southern Nevada and adjacent California (Barneby 1964).

Astragalus lentiginosus Dougl. ex Hook. var. *scorpionis* M. E. Jones, Rev. Astrag. 124. 1923.

Status: Rare and local; possibly threatened.

Distribution: Juab Co., Utah (Schoener 1975), and Nevada (Barneby 1964).

Astragalus lentiginosus Dougl. ex Hook. var. *stramineus* (Rydb.) Barneby, Leafl. W. Bot. 4: 122. 1945, based on *Cystium stramineum* Rydb., N. Amer. Fl. 24: 409. 1929.

Type: Southern Utah, 1870, *Palmer s.n.* (NY).

Status: Locally common, restricted, neither threatened nor endangered.

Distribution: Washington Co., Utah (BRY), Mohave Co., Arizona, and Clark Co., Nevada (Schoener 1975).

Astragalus lentiginosus Dougl. ex Hook. var. *ursinus* (A. Gray) Barneby, Leafl. W. Bot. 4: 133. 1945, based on *A. ursinus* A. Gray, Proc. Amer. Acad. Art 13: 367. 1878.

Type: Bear Valley, in south central Utah, 1877, *Palmer s.n.* (GH).

Status: Endemic, possibly extinct.

Distribution: Iron (or possibly Sevier) Co., Utah; perhaps the specimens are mislabeled.[6]

Astragalus limnocharis Barneby, Leafl. W. Bot. 4: 236. 1946.

Type: Gravelly beach of Navajo Lake, at Spruce Forest Camp, Iron Co., Utah, 13 Jul 1940, *Maguire 19474* (NY).

Status: Endemic, rare and restricted; threatened.

Distribution: Iron and Kane (BRY) counties, Utah (Barneby 1964).

Astragalus loanus Barneby, Mem. New York Bot. Gard. 13: 661. 1964, based on *A. newberryi* var. *wardianus* Barneby, Amer. Midl. Naturalist 37: 481. 1947.

Type: Canyon east of Glenwood, Sevier Co., Utah, 1875, *Ward 223* (GH).

Status: Endemic, rare and threatened (Ripley, E).

Distribution: Garfield, Piute, Sevier and Wayne counties, Utah (BRY).

Astragalus lutosus M. E. Jones, Contr. W. Bot. 13: 7. 1910.

Type: White River, Uintah Co., Utah, 25 May 1958, 5,200 feet, *M. E. Jones s.n.* (POM).

Status: Uinta Basin endemic, rare and edaphically restricted; endangered (Ripley, E).

Distribution: Uintah Co., Utah, and Rio Blanco Co. Colorado (Barneby 1964).

Astragalus malacoides Barneby, Mem. New York Bot. Gard. 13: 500. 1964.

Type: Northeast slope of Kaiparowits Plateau, south of Willow Tank, Kane Co., Utah, 9 May 1939, *Harrison 9069* (US).

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[5] Schoener (1975) has determined that this name includes var. *platyphyllidius* (Rydb.) M. E. Peck, and therefore defines the taxon differently from Ripley (1975).

[6] This variety was reduced to synonymy under var. *palans* (M. E. Jones) M. E. Jones by Schoener (1975), but that taxon is currently known only from the valleys of the Colorado and Virgin rivers. The exaction location of "Bear Valley" has not been determined (McVaugh 1956).

Status: Endemic, restricted though locally common; threatened (Ripley, E).

Distribution: Kane Co., Utah (BRY).

Astragalus minthorniae (Rydb.) Jeps. var. *gracilior* (Barneby) Barneby, Amer. Midl. Naturalist 55: 493. 1956, based on *A. ensiformis* var. *gracilior* Barneby Proc. Calif. Acad. Sci. IV, 25: 158. 1944.

Type: Ca 5 miles south of Veyo, Washington Co., Utah, 4,900 feet, *Ripley & Barneby 4951* (CAS).

Status: Endemic (?), locally common in disjunct populations, possibly threatened (Ripley, E).

Distribution: Washington Co., Utah (BRY), and possibly in Mohave Co., Arizona.

Astragalus monumentalis Barneby, Leafl. W. Bot. 7: 35. 1953.

Type: White Canyon, 25 miles southeast of Hite, San Juan Co., Utah, 18 May 1950. *Harrison 11595* (US).

Status: Endemic, rare and restricted edaphically, possibly threatened.

Distribution: Garfield and San Juan counties, Utah (BRY).

Astragalus musiniensis M. E. Jones, Proc. Calif. Acad. Sci. II, 5: 671. 1895.

Type: San Rafael Swell, Emery (?) Co., Utah, 12 May 1914, *M. E. Jones s.n.* (POM).

Status: Endemic, rare to common, neither threatened nor endangered.

Distribution: Carbon, Emery, Garfield, Grand, and Wayne counties, Utah (BRY).

Astragalus nidularius Barneby, Leafl. W. Bot. 8: 16. 1956.

Type: Near the head of White Canyon, 2 miles below the Kachina Bridge of Natural Bridges N.M., *Barneby 12778* (CAS).

Status: Endemic, restricted and local, disjunct in several main locations, neither threatened nor endangered. (Ripley, T).

Distribution: Garfield, San Juan, and Wayne counties, Utah (BRY).

Astragalus oophorus S. Wats. var. *lonchocalyx* Barneby, Leafl. W. Bot. 7: 194. 1954.

Status: Rare and threatened (Ripley, T).

Distribution: Iron Co., Utah (BRY), and adjacent Nevada (Barneby 1964).

Astragalus pardalinus (Rydb.) Barneby, Mem. New York Bot. Gard. 13: 883. 1964, based on *Phaca pardalina* Rydb., N. Amer. Fl. 24: 352. 1929.

Type: Cedar Mtn., Emery Co., Utah, 20 May 1915, *M. E. Jones s.n.* (NY).

Status: Endemic, restricted though locally common, neither threatened nor endangered (Ripley, E).

Distribution: Emery, Garfield, and Wayne counties, Utah (BRY).

Astragalus perianus Barneby, Mem. New York Bot. Gard. 13: 973. 1964.

Type: Mountains north of Bullion Creek, near Marysvale, Piute Co., Utah, 23 Jul 1905, *Rydberg & Carlton 7104* (NY).

Status: Endemic and threatened (Ripley, PoEx).

Distribution: Piute (Barneby 1964) and Garfield (BRY) counties, Utah.[7]

Astragalus pinonis M. E. Jones, Contr. W. Bot. 8: 14. 1898.

Type: Frisco, Beaver Co., Utah, 22 Jun 1880, ca 8,000 feet, *M. E. Jones s.n.* (POM).

Status: Rare and possibly extirpated.

Distribution: Beaver and Juab counties, Utah, and in east central Nevada (Barneby 1964).

Astragalus platytropis A. Gray, Proc. Amer. Acad. Arts 6: 526. 1865.

Status: Rare and local, both edaphically and altitudinally restricted.

Distribution: Western Beaver (BRY) and Tooele counties, Utah, and much of Nevada and adjacent California (Barneby 1964).

Astragalus rafaelensis M. E. Jones, Rev. Astrag. 146. 1923.

Type: Near Cedar Mtn., Emery Co., Utah, 19 May 1915, *M. E. Jones s.n.* (POM).

Status: Endemic, restricted edaphically, threatened (Ripley, T).

Distribution: San Rafael Swell, Emery Co., Utah (BRY).

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[7] This species, previously known only from the type collection, was rediscovered in 1975: one of many species thought to be extinct but found during 1975 as a result of the interest generated by the Smithsonian Report.

Astragalus sabulosus M. E. Jones, Zoe 2: 239. 1891.

Type: Cisco, Grand Co., Utah, 2 May 1890, *M. E. Jones s.n.* (POM).

Status: Endemic, rare and edaphically restricted; threatened.

Distribution: Grand Co., Utah (BRY; Welsh 1974a).

Astragalus saurinus Barneby, Leafl. W. Bot. 8: 17. 1956.

Type: Dinosaur N.M., 6 miles north of Jensen, Uintah Co., Utah, 26 Jun 1953, *Holmgren & Tillett 9527* (NY).

Status: Endemic, rare and edaphically restricted; threatened (Ripley, E).

Distribution: Uintah Co., Utah (BRY, UTC).

Astragalus serpens M. E. Jones, Proc. Calif. Acad. Sci. II, 5: 641. 1895.

Type: Loa Pass, Wayne Co., Utah, 17 Jul 1894, *M. E. Jones 5639i* (POM).

Status: Endemic, local and periodically abundant in disjunct populations, neither threatened nor endangered (Ripley, E).

Distribution: Garfield, Piute and Wayne counties, Utah (BRY).

Astragalus stocksii Welsh, Great Basin Nat. 34: 307. 1974.

Type: Henry Mts., Penellen Pass, Garfield Co., Utah, 30 May 1972, *Welsh 11740* (BRY).

Status: Endemic, rare and local; threatened.

Distribution: Garfield Co., Utah; known only from the type area (BRY).

Astragalus striatiflorus M. E. Jones, Proc. Calif. Acad. Sci. II, 5: 643. 1895.

Type: Above Springdale, Washington Co., Utah, 25 Sep 1894, 4,000 feet, *M. E. Jones 6080k* (POM).

Status: Rare and edaphically restricted; endangered (Ripley, T).

Distribution: Kane and Washington counties, Utah, and Coconino Co., Arizona (BRY).

A main locality of distribution for this plant is the Coral Pink Dunes region where the plants grow in the interdune valleys. The use of that region for recreation possibly spells the doom of this plant in that section.

Astragalus tephrodes A. Gray var. *brachylobus* (A. Gray) Barneby, Amer. Midl. Naturalist 37: 466. 1947, based on *A. shortianus* var. *brachylobus* A. Gray, Proc. Amer. Acad. Arts 13: 367. 1878.

Status: Rare and possibly extirpated from Utah.

Distribution: Washington Co., Utah (Barneby 1964).

Astragalus tetrapterus A. Gray, Proc. Amer. Acad. Arts 13: 369. 1878.

Type: Ca 25 miles north of St. George, Washington Co., Utah, 1877, *Palmer 111* (GH).

Status: Restricted but locally common to abundant, possibly threatened.

Distribution: Beaver, Iron, Kane, and Washington counties, Utah (BRY); also in northwestern Arizona (BRY), Nevada, and Oregon (Barneby 1964).

Astragalus wardii A. Gray, Proc. Amer. Acad. Arts 12: 55. 1876.

Type: On the edge of the Aquarius Plateau, Sevier Co., Utah, 1875, 8,700 feet, *Ward 424* (GH).

Status: Endemic, local and disjunct, neither threatened nor endangered.

Distribution: Garfield, Kane, Piute, and Sevier counties, Utah (BRY).

Astragalus wetherillii M. E. Jones, Zoe 4: 34. 1893.

Status: Possible extirpated from Utah (Ripley, T).

Distribution: Grand Co., Utah, and west central Colorado (Barneby 1964).

Astragalus woodruffii M. E. Jones, Rev. Astrag. 77. 1923.

Type: On the sandy foot of the San Rafael Swell, Emery (?) Co., Utah, 17-18 May 1914, *M. E. Jones s.n.* (POM).

Status: Endemic, Local and edaphically restricted, possibly threatened.

Distribution: Emery, Wayne, and possibly Garfield counties, Utah (BRY).

Dalea epica Welsh, Great Basin Nat. 31: 90. 1971.

Type: Ca 10 miles east of Halls Crossing, San Juan Co., Utah, 30 Apr 1966, *Welsh 5205* (BRY).

Status: Endemic, restricted and rare, and possibly threatened.

Distribution: San Juan Co., Utah (BRY); known only from the type locality.

Hedysarum boreale Nutt. var. *gremiale* (Rollins) Northstrom & Welsh, Great Basin Nat. 30: 125. 1970, based on *H. gremiale* Rollins, Rhodora 42: 230. 1940.

TYPE: West of Vernal, Uintah Co., Utah, 16 Jun 1937, *Rollins 1733* (GH).

STATUS: Endemic, local and restricted, possibly threatened.

DISTRIBUTION: Duchesne and Uintah counties, Utah (BRY).

Hoffmanseggia repens (Eastw.) Cockerell, Muhlenbergia 4: 68. 1908, based on *Caesalpinia repens* Eastw., Zoe 4: 116. 1893.

TYPE: Court House Wash, near where it comes into the Grand [Colorado] River, near Moab, Grand Co., Utah, 26 May 1892, *Eastwood s.n.* (CAS).

STATUS: Endemic, edaphically restricted but locally common, neither threatened nor endangered, but apparently extirpated from the type area (Harrison et al. 1964).

DISTRIBUTION: Emery (BRY), Grand, and Wayne (BRY) counties, Utah.

Lathyrus brachycalyx Rydb. ssp. *zionis* (C. L. Hitchc.) Welsh, Proc. Utah Acad. Sci. 52: 217. 1966, based on *L. zionis* C. L. Hitchc., Univ. Wash. Publ. Biol. 15: 36. 1952.

TYPE: Ten miles east of the east entrance of Zion N.P., Kane (?) Co., Utah, 30 May 1949, *Hitchcock 19013* (WTU).

STATUS: Rare to locally abundant in disjunct populations, neither threatened nor endangered.

DISTRIBUTION: Grand, Kane, San Juan, and Washington counties, Utah, and Coconino Co., Arizona (BRY); reportedly more widespread in Arizona (McDougall 1973) .

Lotus longebracteatus Rydb., Bull. Torrey Bot. Club 30: 254. 1903.

TYPE: Southern Utah, possibly Washington Co., Utah, 1877, *Palmer 94* (US).

STATUS: Endemic (?), restricted but locally abundant, neither threatened nor endangered.

DISTRIBUTION: Kane and Washington counties, Utah (BRY; Ottley 1944).

Lupinus jonesii Rydb., Bull. Torrey Bot. Club 30: 256. 1903.

TYPE: Silver Reef, Washington Co., Utah, 3 May 1894, *M. E. Jones 5143* (US).

STATUS: Endemic, rare and threatened.

DISTRIBUTION: Washington Co., Utah (BRY).

Lupinus marianus Rydb., Bull. Torrey Bot. Club 34: 41. 1907.

TYPE: Along Bullion Creek above Marysvale, Piute Co., Utah, 21 Jul 1905, *Rydberg & Carlton 7024* (NY).

STATUS: Endemic, restricted and threatened (Ripley, T).

DISTRIBUTION: Piute Co., Utah (BRY).

Oxytropis jonesii Barneby, Proc. Calif. Acad. Sci. IV, 27: 215. 1952.

TYPE: Red Canyon, Garfield Co., Utah, 7 Jun 1947, 7,150 feet, *Ripley & Barneby 8550* (CAS).

STATUS: Endemic, edaphically restricted and threatened.

DISTRIBUTION: Emery (US), Garfield (BRY), Iron (BRY, US) and Uintah (BRY, NY, UTC) counties, Utah.

Oxytropis multiceps Torr. & Gray, Syn. Fl. N. Amer. 1: 341. 1838.

STATUS: Rare and local, possibly endangered.

DISTRIBUTION: Daggett Co., Utah, and in Wyoming and Colorado (Barneby 1952).

Oxytropis obnapiformis C. L. Porter, Madroño 9: 133. 1947.

STATUS: Rare and local, possibly threatened (Ripley, E).

DISTRIBUTION: Daggett Co., Utah; also in Wyoming and Colorado (BRY).

Peteria thompsonae S. Wats., Amer. Naturalist 7: 300. 1873.

TYPE: Kanab, Kane Co., Utah, 1872, *Thompson s.n.* (GH).

STATUS: Restricted in disjunct populations, neither threatened nor endangered (Ripley, T).

DISTRIBUTION: Emery, Grand, Kane, San Juan, and Washington counties, Utah; Mohave Co., Arizona, Nevada, and Idaho (BRY; Porter 1956).

Psoralea aromatica Payson, Bot. Gaz. 60: 379. 1915.

Status: Edaphically restricted, local and rare; possibly threatened.

Distribution: Emery and Grand counties, Utah, and Montrose Co., Colorado (BRY; Ockendon 1965).

Psoralea castorea S. Wats., Proc. Amer. Acad. Arts 14: 291. 1879.

Type: Near Beaver City, Beaver Co., Utah, 1877, *Palmer 96* (GH).[8]

Status: Unknown from Utah in contemporary collection, although a specimen without collector or date labeled *P. castoria* is on file at UT; either extirpated from the state, or, and more likely, never from Utah.

Distribution: Arizona and adjacent southern California (Kearney & Peebles 1951; Munz & Keck 1959).

Psoralea epipsila Barneby, Leafl. W. Bot. 3: 193. 1943.

Type: Ca 17 miles east of Kanab toward Jepson Springs, Kane Co., Utah, 6 Jun 1942, *Ripley & Barneby 4832* (CAS).

Status: Mohave corridor endemic, rare and endangered (Ripley, T).

Distribution: Kane Co., Utah, and adjacent Coconino Co., Arizona (Barneby 1943).

Psoralea juncea Eastw., Proc. Calif. Acad. Sci. II, 6: 286. 1896.

Type: Epsom Creek, San Juan Co., Utah, 13 Jul 1895, *Eastwood 21* (CAS).

Status: Navajo Basin endemic, edaphically restricted but abundant to common, neither threatened nor endangered.

Distribution: Garfield, Kane, and San Juan counties, Utah (BRY), and Coconino Co., Arizona.

Psoralea lanceolata Pursh var. *stenophylla* (Rydb.) Toft & Welsh, Great Basin Nat. 32: 85. 1972, based on *P. stenophylla* Rydb., Bull. Torrey Bot. Club 40: 46. 1913.

Type: Proposed dam site near Wilson Mesa, Grand Co., Utah, 1 Jul 1911, *Rydberg & Garrett 8367* (NY).

Status: Endemic, locally common and neither threatened nor endangered.

Distribution: Garfield, Grand, Kane, San Juan and Wayne counties, Utah (Toft & Welsh 1972).

Psoralea pariensis Welsh & Atwood, spec. nov. *P. megalanthae* Wooton & Standley proxime affinis sed floribus brevioribus et venas supra valde albo-strigosas.

Plantae habentes caudices bene-evoluti et radices tuberosae, 2-8 cm altae; caules 0.5-3 (4.5) cm longi, internodiis 1-3 elongatis, strigosi; stipulae 4-7 (10) mm longae, ovatae vel obovatae, strigosae; foliola 3-5, 9-23 (25) mm longa, 7-22 mm lata, obovata vel orbicularia, cuneata, rotundata ad truncata vel emarginata apicaliter, utrinque glandulifera; petioli 1.3-6.3 (7) cm longi, strigosi, pilis appressis vel adscendentibus; pedunculi 0.5-2.2 (2.8) cm longi, pilis appressis vel adscendentibus; bracteae 4-6 (8) mm longae, ovatae vel obovatae, acuminatae abrupte, pilosae rigide; pedicelli (1) 2-3.8 mm longi, pilis adscendentibus; calyces plus minusve gibbosi basim, tubus 3.3-4 (4.6) mm longus, dentes inaequales, infimis 5.3-6.8 mm longis, circa duplo latioribus quam lateralibus; corolla 8.8-10.5 (12) mm longa, dente infimo calycis leviter longioribus; alae vexillo subaequalis, purpureo-maculatae ad apicem; fructus usque ad 9 mm longum et seminum usque ad 5.2 mm longum.

Type: UTAH: Garfield Co.: Bryce Canyon National Park, in ponderosa pine woods, as ground layer, at ca 8,000 feet elevation, 26 Jun 1975, *Welsh & Murdock 12859*. Holotype, BRY, Isotypes to be distributed.

Additional specimens examined: UTAH: Garfield Co.: East Creek, 3 miles south of Inspiration Point, Bryce Canyon N.P., in black sagebrush area, 11 Jun 1970, *Buchanan 1494* (BRY, WSCO); Paria View, Bryce Canyon N.P., in open ponderosa pine woods, ca 8,000 feet elevation, 12 Jun 1975, *S. L. & S. L. Welsh 12810* (BRY); East Creek, 9 Jun 1931, *Weight B-31/6-305* (BCNP, US). Kane Co.: Hackberry Canyon in Cottonwood Wash, ca 10 miles north of U.S. Highway 89, sec. 31, T. 40S., R. 1W., 26 Apr 1972, *Atwood 3684* (BRY).

Status: Endemic, rare and threatened.

Distribution: Kane and Garfield counties, Utah.

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[8] It seems likely that Palmer mislabled the type material, and that it was in reality from "Beaverdam," Mohave Co., Arizona. The species is not known from Utah.

Parryella filifolia Torr. & Gray in Gray, Proc. Amer. Acad. Arts 7: 397. 1868.

Status: Restricted and rare; threatened.

Distribution: Grand and San Juan counties, Utah (BRY); also in northern Arizona and New Mexico.

Psorothamnus thompsonae (Vail) Welsh & Atwood, comb. nov., based on *Parosela thompsonae* Vail, Bull. Torrey Bot. Club 24: 18. 1897.

Type: Kanab, Kane Co., Utah, or possibly Mohave Co., Arizona, 1872, *Thompson s.n.*[9] (NY).

Status: Endemic (?); restricted but locally common and neither threatened nor endangered.

Distribution: Emery, Garfield, Kane, San Juan, and Wayne counties, Utah (BRY and personal observations).

Robinia neomexicana A. Gray, Mem. Amer. Acad. Arts II, 5: 314. 1855.

Status: Restricted and rare, possibly threatened.

Distribution: Garfield (UT) and Washington counties, Utah (BRY); widespread elsewhere.

Gentianaceae

Gentianella tortuosa (M. E. Jones) Gillett, Ann. Missouri Bot. Gard. 44: 248. 1957, based on *Gentiana tortuosa* M. E. Jones, Proc. Calif. Acad. Sci. II, 5: 707. 1895.

Type: Panguitch Lake, Garfield Co., Utah, 7 Sep 1894, 8,400 feet, *M. E. Jones 6008* (POM).

Status: Restricted but locally common, neither threatened nor endangered.

Distribution: Garfield, Iron, Kane, Sanpete counties, Utah (BRY), and Clark Co., Nevada (Gillett 1957).

Geraniaceae

Geranium marginale Rydb. ex Hanks & Small, N. Amer. Fl. 25: 16. 1907.

Type: Aquarius Plateau at the head of Poison Creek, Garfield Co., Utah, 4 Aug 1905, *Rydberg & Carlton 7401* (NY).

Status: Endemic, restricted and possibly threatened (Ripley, T).

Distribution: Garfield, Sevier, and Wayne counties, Utah (Nebeker 1974).

Hydrophyllaceae

Hydrophyllum fendleri (A. Gray) A. A. Heller, Pl. World 1: 23. 1897, based on *H. occidentale* var. *fendleri* A. Gray, Proc. Amer. Acad. Arts 10: 314. 1875.

Status: Restricted and rare, possibly threatened.

Distribution: San Juan Co., Utah (UT, UTC); widespread from Washington and Oregon to Wyoming, Colorado and New Mexico, with var. *fendleri* restricted to the Rocky Mountain area (Constance 1942).

Nama retrorsum J. T. Howell, Leafl. W. Bot. 5: 149. 1949.

Status: Restricted and local, possibly threatened (Ripley, T).

Distribution: Garfield, Grand, and Kane counties, Utah (BRY), and northeastern Arizona (Atwood, in press).

Nemophila parviflora Dougl. ex Benth. var. *austinae* (Eastw.) A. Brand, Pflanzenr. IV (Heft 251): 55. 1913, based on *N. austinae* Eastw., Bull. Torrey Bot. Club 28: 143. 1901.

Status: Restricted and local, possibly threatened.

Distribution: Weber Co., Utah; widespread in Idaho, Nevada, California, Oregon, and Washington (Atwood, in press).

Phacelia anelsonii J. F. Macbride, Contr. Gray Herb. 49: 26. 1917.

Status: Restricted and local; threatened (Ripley, T).

Distribution: Washington Co., Utah (BRY); southern Nevada and adjacent California (Atwood, in press).

Phacelia argillacea Atwood, Phytologia 26: 437. 1973.

Type: Clear Creek, in Spanish Fork Canyon along the railroad on the east side of U.S. Highway 50-6, Utah Co., Utah, *Atwood et al. 3091* (BRY).

Status: Endemic, rare and endangered (Ripley, E).

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[9] It is likely that some of the collections sent to Gray at Harvard University (who, in turn, gave them to Watson) may not have been collected by Mrs. Thompson, but others with John Wesley Powell. It is known that both Powell and Bishop collected plants and gave them to Ellen Thompson who did not collect outside of the Kanab area of Kane Co., Utah (Cronquist et al. 1972).

DISTRIBUTION: Utah Co., Utah (Atwood 1973, in press).

Phacelia cephalotes A. Gray, Proc. Amer. Acad. Arts 10: 325. 1875.

TYPE: Valley of the Virgin River, Washington Co., Utah, May 1874, *Parry 179* (GH).

STATUS: Restricted and local, possibly threatened (Ripley, T).
DISTRIBUTION: Kane and Washington counties, Utah, and Mohave and Navajo counties, Arizona (Atwood, in press).

Phacelia constancei Atwood, Rhodora 74: 451. 1972.

STATUS: Edaphically restricted and local; threatened (Ripley, T).
DISTRIBUTION: Emery, Garfield, Kane, and San Juan counties, Utah, and Mohave Co., Arizona (Atwood 1975, in press).

Phacelia crenulata Torr. ex Wats. in King var. *angustifolia* Atwood, Great Basin Nat. 35: 158. 1975.

STATUS: Restricted and in disjunct populations, neither threatened nor endangered.

DISTRIBUTION: Beaver, Garfield, and Kane counties, Utah, and in Coconino and Mohave counties, Arizona (Atwood 1975, in press).

Phacelia demissa A. Gray var. *heterotricha* J. T. Howell, Amer. Midl. Naturalist 29: 8. 1943.

TYPE: Marysvale, Piute Co., Utah, 4 Jun 1894, *M. E. Jones 5388a* (POM).

STATUS: Endemic, restricted and possibly threatened (Ripley, T).
DISTRIBUTION: Piute, Sevier, and Wayne counties, Utah (Atwood, in press).

Phacelia howelliana Atwood, Rhodora 74: 456. 1972.

TYPE: Ca 0.4 miles north of Bluff along Utah Highway 163, San Juan Co., Utah, 13 May 1970, *Atwood 2454* (BRY).

STATUS: Endemic, restricted but locally abundant, neither threatened nor endangered.
DISTRIBUTION: Grand and San Juan counties, Utah (BRY; Atwood 1975, in press).

Phacelia indecora J. T. Howell, Amer. Midl. Naturalist 29: 12. 1943.

TYPE: Bluff, San Juan Co., Utah, 24 May 1919, *M. E. Jones s.n.* (CAS).
STATUS: Endemic, rare and endangered (Ripley, T).
DISTRIBUTION: Wayne and San Juan counties, Utah (Atwood, in press).

Phacelia mammillarensis Atwood, Phytologia 26: 437. 1973.

TYPE: Ca 6 miles east of Glen Canyon City, along the road to Warm Creek, Kane Co., Utah, 6 May 1970, *Welsh & Atwood 9809* (BRY).
STATUS: Endemic, edaphically restricted and endangered (Ripley, E).
DISTRIBUTION: Garfield and Kane counties, Utah (Atwood 1975, in press).

Phacelia rafaelensis Atwood, Rhodora 74: 454. 1972.

TYPE: Capitol Reef N.M., Wayne Co., Utah, 12 Jun 1969, *Atwood & Higgins 1834* (BRY).
STATUS: Restricted and local, threatened (Ripley, T).
DISTRIBUTION: Emery, Washington, and Wayne counties, Utah, and Coconino Co., Arizona (Atwood 1975, in press).

Phacelia salina (A. Nels.) J. T. Howell, Leafl. W. Bot. 4: 16. 1944, based on *Emmenanthe salina* A. Nels., Bull. Torrey Bot. Club 24: 381. 1898, a substitute name for *E. foliosa* M. E. Jones, Zoe 4: 278. 1893, not *P. foliosa* Phillip.
TYPE: Deep Creek Valley, above Furber, Tooele Co., Utah, 8 Jun 1891, *M. E. Jones s.n.* (POM).
STATUS: Rare and possibly extirpated from Utah.
DISTRIBUTION: Tooele Co., Utah, and adjacent Nevada and southern Wyoming (Atwood, in press).

Phacelia tetramera J. T. Howell, Leafl. W. Bot. 4: 16. 1944, based on *Emmenanthe pusilla* A. Gray, Proc. Amer. Acad. Arts 11: 87. 1876, not *P. pusilla* Buckley nor Torr.
STATUS: Rare and possibly threatened.
DISTRIBUTION: Weber Co., Utah (*Arnow 3985* [BRY, UT]); also in Nevada, California and Oregon (Howell 1944).

Phacelia utahensis E. G. Voss, Bull. Torrey Bot. Club 64: 135. 1937.

TYPE: Gunnison, Sanpete Co., Utah, 7 Jun 1910, *M. E. Jones s.n.* (POM).

STATUS: Endemic, edaphically restricted and threatened (Ripley, T).

DISTRIBUTION: Carbon (UT), Sanpete, and Sevier counties, Utah (Atwood 1975, in press).

JUNCACEAE

Juncus bryoides F. J. Hermann, Leafl. W. Bot. 5: 117. 1948.

STATUS: Restricted, rare and possibly threatened.

DISTRIBUTION: Salt Lake and Washington counties, Utah, and in California (Hermann 1948).

LAMIACEAE

Stachys rothrockii A. Gray, Proc. Amer. Acad. Arts 12: 82. 1876.

STATUS: Restricted, rare and possibly endangered.

DISTRIBUTION: Near Orderville, Kane Co., Utah (BRY; Barneby 1944), northern New Mexico and Arizona.

LILIACEAE

Agave utahensis Engelm. in King, Rep. Geol. Explor. 40th Parallel 5: 497. 1871.

TYPE: About St. George, Washington Co., Utah, *Palmer s.n.* (MO).

STATUS: Restricted and rare except locally; commercially exploited and possibly endangered. Our plant is var. *utahensis*.

DISTRIBUTION: Washington Co., Utah (BRY); also in Coconino and Mohave counties, Arizona (Breitung 1960).

Allium passeyi Holmgren & Holmgren, Brittonia 26: 309. 1974.

TYPE: Southwest part of Howell Valley, sec. 7, T.11N., R.5W., Box Elder Co., Utah, 13 Jun 1960, 4,800 feet, *Holmgren et al. 13125* (NY).

STATUS: Endemic, rare and endangered (Ripley, E).

DISTRIBUTION: Box Elder Co., Utah; known only from the type locality (Holmgren & Holmgren 1974).

Eremocrinum albomarginatum (M. E. Jones) M. E. Jones, Zoe 4: 53. 1893, based on *Hesperanthes albomarginata* M. E. Jones, Zoe 2: 251. 1891.

TYPE: Green River, Emery Co., Utah, 9 May 1890, *M. E. Jones s.n.* (POM).

STATUS: Navajo Basin endemic, edaphically restricted but locally common to abundant and neither threatened nor endangered.

DISTRIBUTION: Emery, Garfield, Grand, Kane, San Juan, and Wayne counties, Utah, and Apache and Navajo counties, Arizona (MacDougall 1973).

Nolina microcarpa S. Wats., Proc. Amer. Acad. Arts 14: 247. 1879.

STATUS: Apparently extirpated from Utah; last seen in Zion N.P. in 1925 (Cottam 1974).

DISTRIBUTION: Washington Co., Utah, to northern Mexico, eastward to western Texas.

This plant has mistakenly been called *Nolina parryi* (Kearney & Peebles 1951) or *N. bigelovii* (Cottam 1974).

Yucca brevifolia Engelm. in King, Rep. Geol. Explor. 40th Parallel 5: 496. 1871.

STATUS: Restricted but locally abundant; possibly threatened by commercial exploitation.

DISTRIBUTION: Southwestern Washington Co., Utah; western Arizona, southern Nevada and adjacent California (McKelvey 1938; Weber 1953).

Yucca toftiae Welsh, Great Basin Nat. 34: 308. 1974.

TYPE: Three Garden, ca 1 mile north of the confluence of San Juan and Colorado rivers, Lake Powell, San Juan Co., Utah, 4 Jun 1973, *Welsh 11935a* (BRY).

STATUS: Endemic, local and uncommon; possibly threatened.

DISTRIBUTION: Kane and San Juan counties, Utah (BRY); much of the known range of this entity has been inundated by the water of Lake Powell.

Zigadenus vaginatus (Rydb.) J. F. Macbride, Contr. Gray Herb. 53: 4. 1918, based on *Anticlea vaginata* Rydb., Bull. Torrey Bot. Club 39: 108. 1912.

TYPE: Armstrong Canyon, near the Natural Bridges, San Juan Co., Utah, 4-6 Aug 1911. *Rydberg & Garrett 9407* (NY).

STATUS: Endemic, restricted and possibly endangered.

DISTRIBUTION: Grand, Kane, and San Juan counties, Utah (BRY).

This distinctive species was placed in synonymy under the Mexican species, *Zigadenus volcanicus* Benth., Pl. Hartwegianus 96. 1840, by Tidestrom (1925), Tidestrom and Kittell (1941), and followed by Holmgren and Reveal (1967). This plant is related to Z. *elegans* Pursh, but differs in having an elongated paniculate inflorescence and smaller white to greenish flowers borne in the late summer and early fall.

LOASACEAE

Mentzelia argillosa J. Darlington, Ann. Missouri Bot. Gard. 21: 153. 1934.

TYPE: Vermillion, Sevier Co., Utah, 16 Jul 1894, 5,600 feet, *M. E. Jones 5631* (MO).

STATUS: Endemic, edaphically restricted and threatened.

DISTRIBUTION: Sevier Co., Utah (BRY).

Mentzelia obscura Thompson & Roberts, Phytologia 21: 284. 1971.

STATUS: Local and infrequent.

DISTRIBUTION: Washington Co., Utah; southern Nevada and western Arizona westward to California and Baja California, Mexico.

Petalonyx parryi A. Gray, Proc. Amer. Acad. Arts 10: 72. 1874.

TYPE: St. George, Washington Co., Utah, "within a stone's throw of the great Mormon Temple" (see Parry 1875), 1874, *Parry 75* (GH).

STATUS: Rare and possibly endangered.

DISTRIBUTION: Washington Co., Utah (BRY), northern Arizona and southern Nevada (Davis & Thompson 1967).

LOGANIACEAE

Buddleja utahensis Coville, Proc. Biol. Soc. Wash. 7: 69. 1892.

TYPE: Near St. George, Washington Co., Utah, 1877, *Palmer s.n.* (US).

STATUS: Restricted, rare and possibly threatened.

DISTRIBUTION: Washington Co., Utah; also in northwestern Arizona, southern Nevada and southeastern California (Munz 1974).

LORANTHACEAE

Phorandendron californicum Nutt., J. Acad. Nat. Sci. Philadelphia II, 1: 185. 1848.

STATUS: Restricted but locally abundant; neither threatened nor endangered.

DISTRIBUTION: Washington Co., Utah; widespread in Arizona, Nevada, southern California, and northern Mexico (Kearney & Peebles 1951).

MALVACEAE

Sphaeralcea caespitosa M. E. Jones, Contr. W. Bot. 12: 4. 1908.

TYPE: Wah Wah, Beaver Co., Utah, 1906, 6,000 feet, *M. E. Jones s.n.* (POM).

STATUS: Endemic, rare and threatened.

DISTRIBUTION: Beaver and Millard counties, Utah (BRY; Jefferies 1972).

MARTYNIACEAE

Proboscidea louisiana (Miller) Thell., Mém. Soc. Sci. Nat. Cherbourg 3: 480. 1912, based on *Martynia louisiana* Miller, Gard. Dict. ed 8, Martynia No. 3. 1768.

STATUS: Restricted and uncommon, but neither rare nor endangered.

DISTRIBUTION: Washington Co., Utah (BRY); widespread in the southwestern states and elsewhere.

NAJADACEAE

Najas caespitosus (Maguire) Reveal, stat. & comb. nov., based on *Najas flexilis* ssp. *caespitosus* Maguire in Maguire & Jensen, Rhodora 44: 7. 1942.

TYPE: Common in shallow water, Pelican Point, Fish Lake, Sevier Co., Utah, 3 Aug 1940, 8,600 feet, *Maguire 19888* (NY).

STATUS: Endemic and endangered.

DISTRIBUTION: Sevier Co., Utah; known only from the type area (Maguire & Jensen 1942).

Najas guadalupensis Morong, Mem. Torrey Bot. Club 3: 60. 1893.

STATUS: Rare and restricted.

DISTRIBUTION: Cache Co., Utah (UTC; Maguire & Jensen 1942); widespread elsewhere.

NYCTAGINACEAE

Boerhaavia torreyana (S. Wats.) Standley, Contr. U.S. Natl. Herb. 12: 385. 1909, based on *B. spicata* var. *torreyana* S. Wats., Proc. Amer. Acad. Arts 24: 70. 1889.

STATUS: Local, rare and highly restricted; possibly threatened.

DISTRIBUTION: Kane Co., Utah (*Atwood 3389* [BRY, WTS]).

Hermidium alipes S. Wats. var. *pallidum* C. L. Porter, Rhodora 54: 158. 1952.

TYPE: Ca 5 miles south of Vernal, Uintah Co., Utah, 3 Jun 1950, 5,200 feet, *Porter 5308* (RM).

STATUS: Endemic, rare and endangered.

DISTRIBUTION: Uintah Co., Utah (Porter 1952).

OLEACEAE

Menodora scabra A. Gray, Amer. J. Sci. Arts II, 14: 44. 1852.

STATUS: Rare, in disjunct populations, and possibly threatened.

DISTRIBUTION: Garfield and Washington counties, Utah (BRY); widespread in the southwestern states and northern Mexico (Kearney & Peebles 1951).

ONAGRACEAE

Epilobium nevadense Munz, Bull. Torrey Bot. Club 56: 166. 1929.

STATUS: Rare and threatened (Ripley, T).

DISTRIBUTION: Washington Co., Utah (Higgins 1972b), and Clark Co., Nevada.

Oenothera brevipes A. Gray var. *pallidula* Munz, Amer. J. Bot. 15: 229. 1928.

STATUS: Restricted and local, possibly threatened.

DISTRIBUTION: Washington Co., Utah (BRY); also in northwestern Arizona, southern Nevada and southern California (Raven 1969).

Oenothera gouldii (Raven) Welsh & Atwood, comb. nov., based on *Camissonia gouldii* Raven, Contr. U.S. Natl. Herb. 37: 368. 1969.

TYPE: Steep slope of volcanic cone among loose cinders, Diamond Valley, 12 miles north of St. George, Washington Co., Utah, 15 Oct 1941, 3,500 feet, *Gould 1423* (POM).

STATUS: Restricted and rare, possibly threatened.

DISTRIBUTION: Washington Co., Utah, and Coconino Co., Arizona (Raven 1969).

Oenothera megalantha (Munz) Raven, Univ. Calif. Publ. Bot. 34: 111. 1962, based on *O. heterochroma* var. *megalantha* Munz, Leafl. W. Bot. 3: 52. 1941.

STATUS: Restricted and rare, endangered (Ripley, E).

DISTRIBUTION: Kane Co., Utah (BRY), and Nye Co., Utah (Raven 1969; Beatley 1973).

Oenothera parryi S. Wats., Amer. Naturalist 9: 270. 1875.

TYPE: Near St. George, Washington Co., Utah, 1874, *Parry 72* (GH).

STATUS: Restricted but locally abundant (Ripley, T).

DISTRIBUTION: Washington Co., Utah, and adjacent Arizona (BRY).

OPHIOGLOSSACEAE

Botrichium boreale (Fries) Milde var. *obtusilobum* (Rupr.) M. Braun, Index N. Amer. Ferns 33. 1938. Based on *B. crassinervum* var. *obtusilobum* Rupr., Beitr. Pflanzenk. Russ. Reiches 11: 42. 1959.

STATUS: Rare; possibly threatened.

DISTRIBUTION: Summit Co., Utah according to Flowers 1944; not reported from Utah by Cronquist et al. 1972); widespread in northwestern America.

Botrychium lanceolatum (S. G. Gmelin) Ångström, Bot. Not. 1854: 68. 1854, based on *Osmunda lanceolata* S. G. Gmelin, Novi Comment. Acad. Petrop. 12: 516-1768.

STATUS: Rare; possibly threatened.

DISTRIBUTION: Juab Co., Utah (Flowers 1944; Maguire & Holmgren 1946); widely distributed in northern North America (Welsh 1974b).

Botrichium matricariifolium A. Braun in Koch var. *hesperium* (Maxon & Clausen) M. Braun, Index N. Amer. Ferns 39. 1938, based on *B. matricariifolium* ssp. *herperium* Maxon & Clausen, Mem. Torrey Bot. Club 19: 38. 1938.

STATUS: Rare; possibly threatened.

Distribution: Salt Lake Co., Utah (Flowers 1944; not reported by Cronquist et al. 1972 as, in their opinion, Flowers' identification was in error); also in Colorado.

Orchidaceae

Cypripedium calceolus L. var. *parviflorum* (Salisb.) Fern., Rhodora 48: 4. 1946, based on *C. parviflorum* Salisb., Trans. Linn. Soc. London 1: 77. 1791.

Status: Extirpated or endangered.

Distribution: Cache (UTC) and Utah (BRY) counties, Utah; widespread in northern North America.

Cypridedium fasciculatum Kellogg ex Wats., Proc. Amer. Acad. Arts 17: 380. 1882.

Status: Rare and endangered.

Distribution: Salt Lake (BRY) and Summit (Tidestrom 1925) counties, Utah; widespread and rare in Washington, California, Idaho, Montana, Wyoming, and Colorado.

Spiranthes cernua (L.) Rich., Mém. Mus. Hist. Nta. 4: 59. 1818, based on *Ophrys cernua* L., Sp. Pl. 946. 1753.

Status: Extirpated from Utah.

Distribution: Salt Lake Co., Utah (*M. E. Jones 1908* [POM]); widespread in the eastern United States (Correll 1950).

Papaveraceae

Papaver radicatum Rottb., Skr. Kiøbenhavnske Selsk. Laerd. Elsk. 10: 455. 1770.

Status: Rare and restricted.

Distribution: Duchesne Co., Utah (BRY); widespread in northern North America, circumboreal (Welsh 1974b).

Arcotmecon humilis Coville, Proc. Biol. Soc. Wash. 7: 67. 1892.

Type: St. George, Washington Co., Utah, 1874, *Parry s.n.* (GH).

Status: Restricted and rare, endangered (Ripley, E).

Distribution: Washington Co., Utah, and Mohave Co., Arizona (BRY).

Pinaceae

Pinus longaeva D. K. Bailey, Ann. Missouri Bot. Gard. 57: 243. 1970.

Status: Restricted but hardly rare; possibly threatened.

Distribution: Beaver (personal observations), Carbon, Duchesne, Garfield, Iron (personal observations), Kane, Millard, and Washington counties, Utah; also in Nevada and eastern California (Bailey 1970).

Poaceae

Andropogon glomeratus (Walter) Britton, Sterns & Poggenb., Prelim. Cat. Antho. & Pterid. within 100 mi. New York City 67. 1888, based on *Cinna glomerata* Walter, Fl. Carol. 59. 1788.

Status: Rare and possibly extirpated from Utah, previously known only along Lake Powell.

Distribution: Kane and San Juan counties, Utah (BRY); widely distributed in southern and southeastern United States, West Indies, Yucatan and Central America.

Blepharidachne kingii (S. Wats.) Hackel in DC., Monogr. Phanerog. 6: 261. 1889, based on *Eremochloe kingii* S. Wats. in King, Rep. Geol. Explor. 40th Parallel 5: 382. 1871.

Status: Rare and local.

Distribution: Beaver, Millard, and Tooele counties, Utah, and adjacent Nevada (BRY).

Festuca dasyclada Hackel ex. Beal, Grasses N. Amer. 2: 602. 1896.

Type: Joe's Valley, Emery Co., Utah, 1875, *Parry s.n.* (US).

Status: Endemic and possibly endangered (Ripley, PoEx).

Distribution: Emery and Sanpete counties, Utah (N. H. Holmgren, personal communication), and Colorado (N. West, personal communication).[10]

Festuca sororia Piper, Contr. U.S. Natl. Herb. 16: 197. 1913.

Status: Rare and restricted.

Distribution: Southeastern Utah (Hitchcock & Chase 1950).

Helictotrichon mortonianum (Lams.-Scribn.) Henrard, Blumea 3: 429. 1940, based on *Avena mortonianum* Lams.-Scribn., Bot. Gaz. 21: 133. 1896.

Status: Rare and endangered.

Distribution: Utah (Hitchcock &

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[10] Until 1975 this species was known only from the type.

Chase 1950); also in Colorado and New Mexico.

Imperata brevifolia Vasey, Bull. Torrey Bot. Club 13: 26. 1886.

Status: Rare, restricted and endangered or possibly extirpated from Utah.

Distribution: San Juan Co., Utah (bry); California, Nevada, and Mexico (Hitchcock & Chase 1950).

The known localities in Utah where this grass occurred have been inundated by Lake Powell.

Muhlenbergia arsenei Hitchc., Proc. Biol. Soc. Wash. 41: 161. 1928.

Status: Rare and local.

Distribution: Garfield (bry), Kane (bry), San Juan (ut), and Washington (utc) counties, Utah; New Mexico and California (Cottam et al. 1940).

Muhlenbergia curtifolia Lams.-Scribn., Bull. Torrey Bot. Club 38: 328. 1911.

Type: Between Kanab and Carmel, Kane Co., Utah, *M. E. Jones 6047* (us).

Status: Restricted and local, possibly threatened.

Distribution: Garfield, Kane, San Juan, and Washington (ut) counties, Utah (bry, utc); southern Nevada and northern Arizona (Hitchcock & Chase 1950).

Muhlenbergia minutissima (Steudel) Swallen, Contr. U.S. Natl. Herb. 29: 207. 1947, based on *Agrostis minutissima* Steudel, Syn. Pl. Glum. 1: 171. 1854.

Status: Local and rare.

Distribution: Washington Co., Utah (*Atwood & Higgins 5528* [bry]).

Muhlenbergia wrightii Vasey in Coult., Manual Bot. Rocky Mt. Region 409. 1885.

Status: Rare and local.

Distribution: Utah (Hitchcock & Chase 1950); Arizona, Colorado, Oklahoma, New Mexico, and northern Mexico.

Puccinellia simplex Lams.-Scribn., U.S.D.A. Div. Agrostol. Circ. 16: 1. 1899.

Status: Rare and possibly threatened.

Distribution: Weber Co., Utah (*Arnow 3986* [bry]); also in California (Hitchcock & Chase 1950).

Sporobolus pulvinatus Swallen, J. Wash. Acad. Sci. 31: 351. 1941.

Status: Rare and possibly threatened.

Distribution: San Juan Co., Utah (bry); New Mexico, Arizona, Texas and northern Mexico (Hitchcock & Chase 1950).

Polemoniaceae

Gilia caespitosa A. Gray, Proc. Amer. Acad. Arts 12: 80. 1876.

Type: Rabbit Valley on barren cliffs of sandstone, Wayne Co., Utah, 1875, 7,000 feet, *Ward s.n.* (gh).

Status: Endemic, rare and endangered (Ripley, E).

Distribution: Wayne Co., Utah (bry, utc).

Gilia latifolia S. Wats. ex Parry, Amer. Naturalist 9: 347. 1875.

Type: Valley of the Virgin, near St. George, Washington Co., Utah, 1874, *Parry 188* (gh).

Status: Rare and local; possibly threatened.

Distribution: Kane, Wayne, and Washington counties, Utah (bry); Arizona, southern Nevada and southern California (Matthews 1971).

Gilia mcvickerae M. E. Jones, Proc. Calif. Acad. Sci. II, 5: 712. 1895.

Type: Marysvale, Piute Co., Utah, 7,000 feet, *M. E. Jones 5378* (pom).

Status: Endemic, rare and local; threatened (Ripley, T).

Distribution: Piute, Sevier, and Uintah counties, Utah (bry).

Gilia stenothyrsa A. Gray, Proc. Amer. Acad. Arts 8: 276. 1870.

Type: In a clear forest, Uinta Mts., Duchesne or Uintah counties, Utah, 1844, *Frémont s.n.* (gh).

Status: Endemic, locally common and neither threatened nor endangered.

Distribution: Carbon (ut), Emery, Duchesne and Uintah counties, Utah (bry, utc).

Phlox cluteana A. Nels., Amer. J. Bot. 28: 24. 1922.

Status: Rare and local; possibly threatened (Ripley, T).

Distribution: San Juan Co., Utah (bry), and northern Arizona (Kearney & Peebles 1951).

Phlox gladiformis (M. E. Jones) E. Nels., Rev. West. N. Amer. Phloxes 21. 1899, based on *P. longifolia* var. *gladiformis* M. E. Jones, Proc. Calif. Acad. Sci. II, 5: 711. 1895.

TYPE: Cedar City, Iron Co., Utah, 11 May 1894, 6,500 feet, *M. E. Jones 5208c* (POM).

STATUS: Rare and local; possibly threatened (Ripley, T).

DISTRIBUTION: Garfield, Iron, and Washington counties, Utah (BRY), and adjacent Nevada.

Phlox grahamii Wherry, Brittonia 5: 63. 1943.

TYPE: Talus slopes on west side of Green River, south of the mouth of Sand Wash, Uintah Co., Utah, 27 May 1933, *Graham 7884* (CM).

STATUS: Endemic, rare and local; threatened (Ripley, T).

DISTRIBUTION: Uintah Co., Utah; known only from the type locality.

Phlox jonesii Wherry, Notul., Nat. Acad. Nat. Sci. Philadelphia 146: 8. 1944.

TYPE: Zion Canyon, Washington Co., Utah, 7 May 1923, *M. E. Jones s.n.* (US).

STATUS: Endemic, rare and threatened (Ripley, T).

DISTRIBUTION: Washington Co., Utah; known only from the type locality (Wherry 1955).

POLYGONACEAE

Eriogonum ammophilum Reveal, Phytologia 23: 163. 1972.

TYPE: Ca 1.3 miles northwest of Ibex Warm Point, on a dry sandy flat, Millard Co., Utah, 4 Aug 1970, 5,270 feet, *Holmgren & Holmgren 4650* (US).

STATUS: Endemic, rare and local; endangered (Ripley, E).

DISTRIBUTION: Millard Co., Utah (BRY, DERM, UTC).

Eriogonum aretioides Barneby, Leafl. W. Bot. 5: 154. 1949.

TYPE: Bare limestone gravel benches in the foothills of the Escalante Range at Widtsoe, Garfield Co., Utah, 8 Jun 1947, 7,750 feet, *Ripley & Barneby 8570* (CAS).

STATUS: Endemic, edaphically restricted and endangered (Ripley, E).

DISTRIBUTION: Garfield Co., Utah (BRY, UT, UTC).

Eriogonum batemanii M. E. Jones, Contr. W. Bot. 11: 11. 1903.

TYPE: Price, Carbon Co., Utah, 29 Jun 1898, *M. E. Jones s.n.* (POM).

STATUS: Restricted and local, neither threatened nor endangered.

DISTRIBUTION: Carbon, Duchesne, Emery, Garfield, and Uintah counties, Utah, and Rio Blanco Co., Colorado (Reveal 1973a).

Eriogonum brevicaule Nutt. var. *cottamii* (S. Stokes) Reveal, Great Basin Nat. 32: 113. 1972, based on *E. tenellum* ssp. *cottamii* S. Stokes, Gen. Eriog. 70. 1936.

TYPE: Canyons in bottoms of the slopes of West Mtn., Utah Co., Utah, 20 Aug 1925, *Cottam 411* (BRY).

STATUS: Endemic, restricted and rare.

DISTRIBUTION: Juab, Millard, and Utah counties, Utah (BRY, NY, UTC).

Eriogonum brevicaule Nutt. var. *wasatchense* (M. E. Jones) Reveal, Great Basin Nat. 32: 113. 1972, based on *E. wasatchense* M. E. Jones, Contr. W. Bot. 11: 11. 1903.

TYPE: American Fork Canyon, Utah Co., Utah, 27 Jul 1880, *M. E. Jones 1877* (POM).

STATUS: Endemic, restricted and rare.

DISTRIBUTION: Davis, Juab, Millard, Salt Lake, Utah, and Weber counties, Utah (BRY, DS, GH, UT, UTC).

Eriogonum clavellatum Small, Bull. Torrey Bot. Club 25: 48. 1898.

TYPE: Barton Range, San Juan Co., Utah, 13 Jul 1895, *Eastwood 132* (NY).

STATUS: Rare and highly restricted; threatened (Ripley, T).

DISTRIBUTION: San Juan Co., Utah (BRY, UTC), and Montezuma Co., Colorado (CS).

Eriogonum contortum Small ex Rydb., Agric. Exp. Sta. Agric. Coll. Colorado Bull. (Fl. Colorado) 100: 107. 1906.

STATUS: Infrequent but neither threatened nor endangered.

DISTRIBUTION: Grand Valley endemic in Grand Co., Utah (BRY, UTC), and Garfield and Mesa counties, Colorado.

Eriogonum corymbosum Benth. in DC. var. *davidsei* Reveal, Great Basin Nat. 27: 216. 1968.

Type: Ca 0.7 miles south of U.S. Highway 50-6 at Wellington, just south of the Price River bridge, 9 Sep 1967, *Reveal & Davidse 956* (UTC).

Status: Endemic, restricted and local; endangered (Ripley, E).

Distribution: Carbon Co., Utah; known only from type locality.

Eriogonum corymbosum Benth. in DC. var. *divaricatum* Torr. & Gray in Beckwith, Explor. & Surv. Railroad Route from Mississippi River to Pacific Ocean 2: 29. 1857.

Type: Near Green River, Emery Co., Utah, 1 Oct 1853, *Creutzfeldt s.n.* (NY).

Status: Endemic, local and restricted; neither endangered nor threatened.

Distribution: Emery, Garfield, and Grand counties, Utah.

This form of *Eriogonum corymbosum* differs from var. *corymbosum* in having small, usually crenulate leaves, smaller more compact stature, and compact inflorescences.

Eriogonum corymbosum Benth. in DC. var. *revealianum* (Welsh) Reveal, stat. & comb. nov., based on *E. revealianum* Welsh, Great Basin Nat. 30: 17. 1970.

Type: Gravelly, boulder-strewn, east-facing slope near the head of the canyon at milepost 26 south of Antimony along Utah Highway 22, Garfield Co., Utah, 4 Sep 1969, *S. L. & S. L. Welsh 9389* (BRY).

Status: Endemic, rare and local; endangered.

Distribution: Garfield Co., Utah; known only from the type locality.

This form of *Eriogonum corymbosum* differs from var. *corymbosum* in having elongated, entire leaves concentrated near the base of elongated flowering stems and open, spreading inflorescences.

Eriogonum cronquistii Reveal, Madroño 19: 289. 1969.

Type: Loose decomposed granite talus slopes on the west side of Bull Mtn., Henry Mts., Garfield Co., Utah, 14 Aug 1967, 8,300 feet, *Holmgren & Reveal 3010* (UTC).

Status: Endemic, restricted and local; endangered (Ripley, E).

Distribution: Garfield Co., Utah; known only from the type locality (BRY, NY, UTC).

Eriogonum desertorum (Maguire) R. J. Davis, Fl. Idaho 246. 1952, based on *E. chrysocephalum* ssp. *desertorum* Maguire, Leafl. W. Bot. 3: 11. 1941.

Status: Restricted and rare; possibly threatened.

Distribution: Box Elder and Tooele counties, Utah; northeastern Nevada and southern Idaho (Reveal 1973a).

Eriogonum ephedroides Reveal, Madroño 19: 295. 1969.

Type: Ca 10 miles south of Bonanza along Utah Highway 45 south of the White River, 25 Jul 1965, *Holmgren et al. 2265* (UTC).

Status: Uinta Basin endemic, restricted and rare; endangered (Ripley, E).

Distribution: Uintah Co., Utah (BRY, UTC), and Rio Blanco Co., Colorado (NY).

Eriogonum eremicum Reveal, Phytologia 23: 165. 1972.

Type: Ca 17 miles southeast of Garrison along Utah Highway 21, Millard Co., Utah, 23 Jul 1965, *Holmgren et al. 2247* (UTC).

Status: Endemic, restricted and rare; threatened (Ripley, T).

Distribution: Millard Co., Utah (BRY, UTC).

Eriogonum fasciculatum Benth. var. *polifolium* (Benth. in DC.) Torr. & Gray, Proc. Amer. Acad. Arts 8: 169. 1870, based on *E. polifolium* Benth. in DC., Prodr. 14: 12. 1856.

Status: Local and common to abundant, neither threatened nor endangered.

Distribution: Emery (BRY, UT; where rare) and Washington (where common) counties, Utah; widespread and common in Arizona, Nevada, California, and Baja California, Mexico.

Eriogonum grayi Reveal, Phytologia 25: 193. 1973.

Type: Lake Blanche, Salt Lake Co., Utah, 15 Aug 1947, *Holmgren et al. 7121* (UTC).

STATUS: Endemic, disjunct and infrequent.

DISTRIBUTION: Juab, Salt Lake, Utah, and Weber counties, Utah (BRY, WSCO, UTC; Reveal 1973a).

Eriogonum humivagans Reveal, Madroño 19: 219. 1969.

TYPE: Ca 13.5 miles east of Monticello, 13 Aug 1966, 6,800 feet, *Holmgren & Reveal 3001* (UTC).

STATUS: Endemic, restricted and rare; endangered (Ripley, E).

DISTRIBUTION: San Juan Co., Utah; known only from the type locality.

Eriogonum hylophilum Reveal & Brotherson, Great Basin Nat. 27: 190. 1968.

TYPE: Along Utah Highway 53 in Gate Canyon, 2.7 miles southwest of the summit of the Badlands Cliffs, Duchesne Co., Utah, 15 Aug 1966, 6,500 feet, *Holmgren & Reveal 3017* (UTC).

STATUS: Endemic, rare and restricted; endangered (Ripley, E).

DISTRIBUTION: Duchesne Co., Utah (Reveal 1968a; 1973a).

Eriogonum intermontanum Reveal, Madroño 19: 293. 1969.

TYPE: Ca 1.5 miles south of the Uintah Co. line at the head of Middle Canyon of West Water Creek drainage in Roan Cliffs, Grand Co., Utah, 27 Jul 1965, 8,400 feet, *Holmgren et al. 2278* (UTC).

STATUS: Endemic, rare and local; endangered (Ripley, E).

DISTRIBUTION: Grand Co., Utah (BRY, UTC).

Eriogonum jamesii Benth. in DC. var. *rupicola* Reveal, Phytologia 25: 202. 1973.

TYPE: Along Utah Highway 15, 4.9 miles west of the east entrance to the park on Checkerboard Mesa, Zion N.P., Washington Co., Utah, 12 Aug 1972, *Reveal & Reveal 2874* (US).

STATUS: Endemic, restricted and rare; threatened (Ripley, T).

DISTRIBUTION: Kane and Washington counties, Utah (Reveal 1973a).

Eriogonum lancifolium Reveal & Brotherson, Great Basin Nat. 27: 188. 1968.

TYPE: On low hills 5 miles east of Wellington, Carbon Co., Utah, 9 Sep 1967, *Reveal & Davidse 957* (UTC).

STATUS: Endemic, restricted and local; threatened (Ripley, E).

DISTRIBUTION: Carbon Co., Utah (BRY, US, UTC).

Eriogonum leptocladon Torr. & Gray in Beckwith, Explor. & Surv. Railroad Route from Mississippi River to Pacific Ocean 2: 129. 1857.

TYPE: Near the Green River, Emery Co., Utah, 1 Oct 1853, *Creutzfeldt s.n.* (NY).

STATUS: Endemic, edaphically restricted but locally abundant and neither threatened nor endangered. Our plant is var. *leptocladon.*

DISTRIBUTION: Emery, Garfield, Grand, San Juan, and Wayne counties, Utah (BRY, UTC; Reveal 1966).

Eriogonum leptophyllum (Torr. & Gray) Wooton & Standley, Contr. U.S. Natl. Herb. 16: 118. 1913, based on *E. effusum* var. *leptophyllum* Torr. in Sitgr., Rep. Exped. Down Zuñi & Colorado rivers 168. 1853.

STATUS: Local and rare; threatened.

DISTRIBUTION: San Juan Co., Utah (*Harrison 12163* [BRY]); southwestern Colorado, northeastern Arizona and adjacent New Mexico (Reveal 1968a).

Eriogonum loganum A. Nels., Bot. Gaz. 54: 149. 1912.

TYPE: Logan, Cache Co., Utah, 26 Jun 1909, *Smith 1704* (RM).

STATUS: Endemic, extremely restricted and rare; endangered (Ripley, E).

DISTRIBUTION: Cache Co., Utah (BRY, UTC).

Eriogonum nanum Reveal, Phytologia 25: 194. 1973.

TYPE: Talus slopes and limestone outcrops south of Willard Peak, Box Elder Co., Utah, 31 Aug 1964, 9,500 feet, *Reveal & Holmgren 665* (US).

STATUS: Endemic, restricted and rare; threatened (Ripley, T).

DISTRIBUTION: Box Elder and Weber counties, Utah (BRY, UTC, WSCO).

Eriogonum natum Reveal, spec. nov.

A *Eriogono brevicaule* Nutt. differt foliis ellipticis, 2-2.5 (3) cm longis et (8) 10-13 (15) mm latis, lanatis, inflorescentiis cymoso-umbellatis, floribus flavis, 2-2.5 (3) mm longis, glabris.

Spreading herbaceous perennials 1-3.5

dm high, 1-4 dm across, with a short woody caudex arising from a stoutish, woody taproot; leaves essentially basal, the leaf-blade elliptic, 2-2.5 (3) cm long, (8) 10-13 (15) mm wide, densely tomentose below, somewhat less so and greenish-tomentose above, the petiole (1) 2-3 cm long, tomentose; flowering stems erect to spreading, slender, 1-2 (2.5) dm long, white to greenish-tomentose; inflorescences cymose-umbellate, 3-10 (15) cm long, 3-5 (8) cm wide, trichotomously branched throughout, tomentose; bracts scalelike to foliaceous, ternate, the former 1-3 mm long, tomentose to floccose without, tomentose within, the latter 1-3 per node, linear-lanceolate to lanceolate, 5-10 (12) mm long, (1.5) 2-4 (5) mm wide, tomentose; peduncles lacking; involucres solitary or infrequently in groups of 2, turbinate-campanulate, 2.5-4 mm long, 2-3 mm wide, thinly to densely tomentose without, glabrous within, the 5 acute teeth 0.5-0.8 mm long, usually with a membranaceous margin, the bractlets linear-oblanceolate, 1.5-3 mm long, fringed with gland-tipped cells, the pedicels 2.5-5 mm long, glabrous; flowers bright yellow with golden yellow bases and golden to greenish midribs, 2-2.5 (3) mm long, glabrous, the tepals oblong to obovate, distinctly keeled at the base and along the midrib of each tepal, united about ¼ to ⅓ the length of the flower; stamens exserted, 2.5-4 mm long, the filaments sparsely pilose basally, the anthers yellow, 0.3-0.5 mm long, oblong to oval; achenes light brown, 2-3 mm long, the globose base tapering to a long, 3-angled, slightly roughened beak.

Type: UTAH: Millard Co.: Along U.S. Highway 50-6, 46.2 miles east of the Nevada state line and about 43 miles west of Delta, on low white alkaline clay outcrops 50-300 meters north of the highway, ca 0.2 miles east of the dirt road junction to the Antelope Spring-Black Hill Well roads, north-northwest of Sevier Lake, 13 Aug 1975, *Reveal & Reveal 3924*. Holotype, US! Isotypes, ARIZ, ASU, BRY, CAS, COLO, GH, ISC, K, MARY, MO, NY, OKL, OSC, PH, RM, RSA, SMU, TEX, UC, UTC, WTU!

Additional specimens examined: UTAH: Millard Co.: Ca 43 miles west of Delta, 30 Aug 1975, *Reveal & Reveal 3999* (BRY, CAS, GH, NY, OKL, RSA, US, UTC); ca 29.8 miles west of Delta, 30 Aug 1975, *Reveal & Reveal 4000* (ARIZ, ASU, BRY, CAS, GH, ISC, MARY, MO, NY, OKL, OSC, RM, RSA, SMU, TEX, US, UTC, WTU).

Eriogonum natum belongs to the large species group typified by *E. brevicaule* and is seemingly most closely related to *E. brevicaule* var. *cottamii* (S. Stokes) Reveal, a narrowly restricted variant of the pinyon-juniper woodlands of north central Utah. The new species differs from var. *cottamii* in having longer and broader elliptical leaves, a longer but less branched inflorescence, and smaller flowers. The new species is restricted to the white alkaline beaches of Sevier Lake and is currently known for the two locations cited above.

Eriogonum natum is named to honor its discoverer, Mark L. Reveal (1961-).

Status: Endemic, rare and threatened.

Distribution: Millard Co., Utah.

Eriogonum nummulare M. E. Jones, Contr. W. Bot. 11. 13. 1903.

Type: Dutch Mtn., Tooele Co., Utah, 15 Jun 1900, *M. E. Jones s.n.* (POM).

Status: Endemic, rare and seemingly local.

Distribution: Juab, Millard, and Tooele counties, Utah (Reveal 1973a).

Eriogonum ostlundii M. E. Jones, Contr. W. Bot. 11: 12. 1903.

Type: Near Joseph City, Sevier Co., Utah, 13 Jun 1898, *M. E. Jones s.n.* (POM).

Status: Endemic, restricted and local; threatened (Ripley, T).

Distribution: Piute and Sevier counties, Utah (Reveal 1973a).

Eriogonum panguicense (M. E. Jones) Reveal, Proc. Utah Acad. Sci. 42: 291. 1966, based on *E. pauciflorum* var. *panguicense* M. E. Jones, Contr. W. Bot. 11: 9. 1903.

Type: Panguitch, Garfield Co., Utah, 24 Jun 1890, *M. E. Jones s.n.* (POM).

Status: Endemic, restricted and local.

Distribution: Garfield, Iron, Kane, Sevier, and Washington counties, Utah (Reveal 1966; 1973a).

Eriogonum panguicense (M. E. Jones) Reveal var. *alpestre* (S. Stokes) Reveal, Proc. Utah Acad. Sci. 42: 292. 1966, based on *E. chrysocephalum* ssp. *alpestre* S. Stokes, Gen. Eriog. 93. 1936.

TYPE: Cedar Breaks N.M., Iron Co., Utah, 18 Jul 1930, *Goodman & Hitchcock 1601* (CAS).

STATUS: Endemic, rare and local; threatened (Ripley, T).

DISTRIBUTION: Iron Co., Utah (BRY, US, UTC).

Eriogonum pharnaceoides Torr. in Sitgr. var. *cervinum* Reveal, Great Basin Nat. 34: 245. 1974.

TYPE: Foothills south of Pinto on the north slope of the Pine Valley Mts., 18 Aug 1973, *Atwood & Higgins 5895* (US).

STATUS: Rare, in disjunct populations.

DISTRIBUTION: Millard and Washington counties, Utah, and in Mohave Co., Arizona, and Lincoln Co., Nevada (Reveal 1974).

Eriogonum plumatella Dur. & Hilg., J. Acad. Nat. Sci. Philadelphia II, 3: 45. 1855.

STATUS: Probably extirpated from Utah.

DISTRIBUTION: "Utah" (*Palmer s.n.* [GH]); infrequent and widely scattered in northwestern Arizona, southern Nevada and southeastern California.

Eriogonum saurinum Reveal, Great Basin Nat. 27: 197. 1968.

TYPE: Along the Island Park road, 10 miles east of Vernal along Brush Creek on steep hillsides on the ridges, Uintah Co., Utah, 15 Aug 1966, 5,200 feet, *Holmgren & Reveal 3019* (UTC).

STATUS: Edaphically restricted; threatened (Ripley, T).

DISTRIBUTION: Uintah Co., Utah, and adjacent northwestern Colorado (Reveal 1973a).

Eriogonum smithii Reveal, Great Basin Nat. 24: 202. 1968.

TYPE: Between Little Flat Top and Big Flat Top, San Rafael Desert, ca 10 miles southeast of Utah Highway 24, Emery Co., Utah, 14 Aug 1966, 5,500 feet, *Holmgren & Reveal 3012* (UTC).

STATUS: Endemic, edaphically restricted and local; threatened (Ripley, T).

DISTRIBUTION: Emery Co., Utah (BRY, UTC).

Eriogonum spathulatum A. Gray, Proc. Amer. Acad. Arts 10: 76. 1874.

TYPE: Lower Valley of the Sevier River, Sevier Co., Utah, Jul 1874, *Parry 245* (GH).

STATUS: Endemic and scattered in isolated populations, but neither threatened nor endangered.

DISTRIBUTION: Beaver, Iron, Millard, Piute, Sanpete, and Sevier counties, Utah (Reveal 1973a).

Eriogonum thompsonae S. Wats., Amer. Naturalist 7: 302. 1873.

TYPE: Sandstone cliffs near Kanab, Kane Co., Utah, 1872, *Thompson s.n.* (GH).

STATUS: Arizona strip endemic, restricted and rare; threatened (Ripley, T).

DISTRIBUTION: Kane and Washington counties, Utah (BRY, MARY, UTC), and Mohave Co., Arizona (BRY, CAS, US, UTC).

Eriogonum thompsonae S. Wats. var. *albiflorum* Reveal, Madroño 19: 299. 1969.

TYPE: Ca 3 miles west of Virgin, Washington Co., Utah, 11 Aug 1966, 3,700 feet, *Holmgren & Reveal 2991* (UTC).

STATUS: Endemic, edaphically restricted and threatened (Ripley, T).

DISTRIBUTION: Washington Co., Utah (BRY, UTC).

Eriogonum tumulosum (Barneby) Reveal, Phytologia 23: 173. 1972, based on *E. villiflorum* A. Gray var. *tumulosum* Barneby, Leafl. W. Bot. 5: 153. 1949.

TYPE: Sandstone ledges and rock-pavement on Red Plateau, southwest of Woodside, Emery Co., Utah, 13 Jun 1947, *Ripley & Barneby 8678* (CAS).

STATUS: Restricted and very local in disjunct populations.

DISTRIBUTION: Duchesne and Emery counties, Utah, and in Moffat Co., Colorado (CS).

Eriogonum umbellatum Torr. Var. *deserticum* Reveal, var. nov. A var. *umbellato* foliis glabris et floribus stramineis differt.

TYPE: UTAH: Utah Co.: Along the Timpooneke Road, 1 mile northwest of Utah Highway 80, near Timpooneke Campground, east of Mt. Timpanogos, associated with Quercus, Populus and Artemisia at about 7,600 feet, 10 Jul 1974, *Reveal 3702*. Holotype, US! Isotypes, BRY, CAS, GH, MARY, MO, NY, OKL, UTC!

STATUS: Endemic, locally common, but neither threatened nor endangered.

DISTRIBUTION: Juab, Salt Lake, Sanpete, Tooele, Utah, and Wasatch counties, Utah.

This form of *Eriogonum umbellatum* has been confused with var. *dichrocephalum* Gandoger which has leaves pubescent at least on the lower surface.

Eriogonum viridulum Reveal, Proc. Utah Acad. Sci. 42: 287. 1966.

TYPE: Ca 8 miles east of Duchesne along U.S. Highway 40, Duchesne Co., Utah, 2 Sep 1964, *Reveal 675* (UTC).

STATUS: Uinta Basin endemic, restricted and local; threatened (Ripley, T).

DISTRIBUTION: Duchesne and Uintah counties, Utah, and Moffat Co., Colorado (Reveal 1973a).

Eriogonum zionis J. T. Howell, Leafl. W. Bot. 2: 253. 1940.

TYPE: Zion N.P. along the Mt. Carmel highway in the canyon of Clear Creek, Washington Co., Utah, 8 Sep 1938, *Eastwood & Howell 6344* (CAS).

STATUS: Endemic, rare and local; endangered (Ripley, E).

DISTRIBUTION: Kane and Washington counties, Utah (for var. *zionis*), with var. *coccineum* J. T. Howell restricted to northern Arizona.

Polygonum utahense Brenckle & Cottam, Bull. Univ. Utah, Biol. Ser. 4(4):3. 1940.

TYPE: Ca 6 miles north of Escalante, Garfield Co., Utah, 17 Sep 1935, *Cottam 6507* (UT).

STATUS: Endemic; species of uncertain taxonomic status.

DISTRIBUTION: Garfield Co., Utah (BRY, UT); known only from the type locality.

POLYPODIACEAE

Asplenium adiantum-nigrum L., Sp. Pl. 1081. 1753.

STATUS: Rare and local; status uncertain within Utah as not collected since the 1930s (Flowers 1944).

DISTRIBUTION: Washington Co., Utah; widespread in Eurasia, known only from three locations in the United States (Cronquist et al. 1972).

Asplenium resiliens Kunze, Linnaea 18: 331. 1844, based on *A. parvulum* Martens & Galeotti, Mém. Foug. Mex. 60. 1842, not Hook.

STATUS: Local and rare; possibly threatened.

DISTRIBUTION: San Juan Co., Utah (Flowers 1965); widespread in North and South America.

Asplenium septentrionale L., Sp. Pl. 1068. 1753.

STATUS: Rare and obscure; possibly endangered.

DISTRIBUTION: Daggett (*Wieboldt 1460A* [UTC]) and Grand (Maguire 1935) counties, Utah; circumboreal.

Notholaena jonesii Maxon, Amer. Fern. J. 7: 108. 1917.

STATUS: Restricted and rare; possibly threatened.

DISTRIBUTION: Washington Co., Utah (Maxon 1917); Arizona and southern California (Flowers 1944; Cronquist et al. 1972).

PORTULACACEAE

Calyptridium monandrum Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 198. 1838.

STATUS: Rare and restricted; possibly threatened.

DISTRIBUTION: Washington Co., Utah (BRY); also Arizona and California, and Baja California, Mexico.

Talinum validulum Greene, Leafl. Bot. Observ. Crit. 2: 270. 1912.

STATUS: Rare and obscure; possibly threatened.

DISTRIBUTION: Emery Co., Utah (BRY); Coconino Co., Arizona.

PRIMULACEAE

Primula incana M. E. Jones, Proc. Calif. Acad. Sci. II, 5: 706. 1895.

TYPE: Beaver Co-op Ranch, at the head of the South Fork of the East Fork of the Sevier River, Garfield Co., Utah, in cold bogs, 7,000 feet, *M. E. Jones 5312av* (POM).

STATUS: Rare and possibly extirpated in the type area; threatened.

DISTRIBUTION: Daggett and Garfield counties, Utah (Cosgriff 1968); widespread in northwestern North America (Welsh 1974b).

Primula maguirei L. O. Williams, Amer. Midl. Naturalist 17: 747. 1936.

TYPE: Damp overhanging rock ledges and cracks, 5 miles up Logan Canyon, Cache Co., Utah, 19 Apr 1932, *Maguire & Maguire 3650* (MO).

STATUS: Endemic, rare and threatened (Ripley, T).

DISTRIBUTION: Cache Co., Utah (UTC).

Primula specuicola Rydb., Bull. Torrey Bot. Club 40: 461. 1913.

TYPE: Along the San Juan River near Bluff, San Juan Co., Utah, 25-29 Aug 1911, *Rydberg 9882* (NY).

STATUS: Restricted habitatwise, local and threatened (Ripley, T).

DISTRIBUTION: Garfield (UT), Grand, Kane, San Juan, and Wayne counties, Utah, and in northern Arizona (Cosgriff 1968; McDougall 1973).

RANUNCULACEAE

Aquilegia micrantha Eastw., Proc. Calif. Acad. Sci. II, 4: 559. 1895.

TYPE: Near Bluff, San Juan Co., Utah, Jul 1894, *Wetherill s.n.* (CAS).

STATUS: Restricted habitatwise, local but not threatened nor endangered.

DISTRIBUTION: Emery, Garfield, Grand, Kane, and San Juan counties, Utah (BRY); also in Arizona and Colorado.

Ranunculus acriformis A. Gray var. *aestivalis* L. Benson, Amer. Midl. Naturalist 40: 43. 1948.

TYPE: Meadow at springs just east of U.S. Highway 89 and 300 yards west of the Sevier River, 8.3 miles north of the principal intersection in Panguitch and about 1.5 miles south of the intersection with Utah Highway 20 leading to Parowan, Garfield Co., Utah, 29 Aug 1948, 6,400 feet, *Benson 13420* (POM).

STATUS: Endemic and presumed to be extinct (Ripley, PoEx).

DISTRIBUTION: Garfield Co., Utah (BRY); known only from the type locality.

ROSACEAE

Chamaerhodos erecta (L). Bunge in Ledeb., Fl. Altaica 1: 430. 1829, based on *Sibbaldia erecta* L., Sp. Pl. 1: 284. 1753.

STATUS: Rare and local, altitudinally restricted.

DISTRIBUTION: Piute and Wayne counties, Utah (BRY); also from Colorado, North Dakota and Michigan, north to Yukon and Alaska; Asia (Welsh 1974b).

Crataegus chrysocarpa Ashe, North Carolina Agric. Exp. Sta. Techn. Publ. 175: 110. 1900, based on *C. rotundifolia* Moench, Verz. Ausl. Baume Staud Weiss 29. 1785, not Lam.

STATUS: Rare and threatened.

DISTRIBUTION: Cache Co., Utah (Maguire 1937); widespread elsewhere.

Crataegus succulenta Schrader ex Link, Handbuch 2: 78. 1831.

STATUS: Local and rare; threatened.

DISTRIBUTION: Utah Co., Utah (BRY, UTC; Barnes 1943); widespread to the east of Utah (Little 1953).

Ivesia sabulosa (M. E. Jones) Keck, Lloydia 1: 124. 1938, based on *Pontentilla sabulosa* M. E. Jones, Proc. Calif. Acad. Sci. II, 5: 680. 1895.

TYPE: Head of the Sevier River, probably in Garfield Co., Utah, 11 Sep 1894, 8,000 feet, *M. E. Jones 6032* (POM).

STATUS: Rare and local, possibly threatened.

DISTRIBUTION: Garfield and Washington counties, Utah (BRY), and Nye Co., Nevada (Keck 1938b).

Ivesia utahensis S. Wats., Proc. Amer. Acad. Arts 17: 371. 1882.

TYPE: On the summit of Bald Mountain, in Wasatch Range, above Alta, Salt Lake Co., Utah, Aug 1879, over 12,000 feet, *M. E. Jones 1231* (GH).

STATUS: Endemic, rare and local.

DISTRIBUTION: Salt Lake, Summit, and Utah counties, Utah (Keck 1938b).

Rubus neomexicanus A. Gray, Smithsonian Contr. Knowl. 5: 55. 1853.

STATUS: Local, rare and threatened.

DISTRIBUTION: San Juan Co., Utah (BRY); New Mexico, Arizona, and northern Mexico.

Most of the known range of this species has been destroyed by Lake Powell.

RUBIACEAE

Galium multiflorum Kellogg var. *watsonii* A. Gray, Syn. Fl. N. Amer. 1: 40. 1884.

TYPE: Wasatch Mts., Utah, 1869, *Watson 484* (GH).

STATUS: Endemic, neither threatened nor endangered.

DISTRIBUTION: Box Elder, Cache, Davis, Tooele, and Utah counties, Utah (Dempster & Ehrendorfer 1965).

Galium scabruisculum (Ehrendorfer) Dempster & Ehrendorfer, Brittonia 17: 312. 1965, based on *G. hypotrichium* ssp. *scabruisculum* Ehrendorfer, Contr. Dudley Herb. 5: 13. 1956.

TYPE: Calf Springs Wash, San Rafael Swell, Emery Co., Utah, *Maguire 18437* (GH).

STATUS: Endemic, neither threatened nor endangered.

DISTRIBUTION: Carbon and Emery counties, Utah.

RUTACEAE

Ptelea trifoliata L. ssp. *pallida* (Greene) V. L. Bailey, Brittonia 14: 23. 1962, based on *P. pallida* Greene, Contr. U. S. Natl. Herb. 10: 70. 1906.

STATUS: Rare and possibly extirpated.

DISTRIBUTION: Garfield and Kane counties, Utah; this subspecies also in Arizona and Colorado (Bailey 1962).

SCROPHULARIACEAE

Castilleja aquariensis N. H. Holmgren, Bull. Torrey Bot. Club 100: 87. 1973.

TYPE: Aquaris Plateau, 22 miles northwest-north of Escalante on the road to Bicknell, 0.5 mile north of Clayton Guard Station turnoff, Garfield Co., Utah, 11 Aug 1970, 9,600 feet, *Holmgren & Holmgren 4726* (NY).

STATUS: Endemic, rare and local; endangered (Ripley, E).

DISTRIBUTION: Garfield Co., Utah; known only from the type area.

Castilleja leonardii Rydb., Bull. Torrey Bot. Club 34: 36. 1907.

TYPE: Head of American Fork Canyon, Utah Co., Utah, 1885, *Leonard 151* (NY).

STATUS: Endemic, locally common but neither threatened nor endangered.

DISTRIBUTION: Cache, Daggett, Davis, Duchesne, Salt Lake, Sanpete, Summit, Tooele, Utah, and Wasatch counties, Utah (BRY, UT).

Castilleja parvula Rydb., Bull. Torrey Bot. Club 34: 40. 1907.

TYPE: Mountains north of Bullion Creek near Marysvale, Piute Co., Utah, 1905, *Rydberg & Carlton 7158* (NY).

STATUS: Endemic, rare and local; threatened (Ripley, T).

DISTRIBUTION: Piute Co., Utah (NY, UTC).

Castilleja revealii N. H. Holmgren, Bull. Torrey Bot. Club 100: 87. 1973.

TYPE: Bryce Canyon N.P., along the road to Bryce Point, 0.5 mile from Inspiration Point turnoff, Garfield Co., Utah, 24 Jun 1965, 8,000 feet, *Holmgren & Reveal 2017* (NY).

STATUS: Endemic, rare and local; endangered (Ripley, E).

DISTRIBUTION: Garfield Co., Utah; known only from the type locality.

Mimulus eastwoodiae Rydb., Bull. Torrey Bot. Club 40: 483. 1913.

TYPE: In crevices of perpendicular or overhanging rocks along the San Juan River near Bluff, 25-29 Aug 1911, *Rydberg 9883* (NY).

STATUS: Edaphically restricted, local and disjunct; not threatened nor endangered.

DISTRIBUTION: Grand, Kane, and San Juan counties, Utah (BRY), and adjacent northern Arizona (Kearney & Peebles 1951).

Penstemon abietinus Pennell, Contr. U.S. Natl. Herb. 20: 276. 1920.

TYPE: Ireland Ranch, head of Salina Canyon, Sevier Co., Utah, 15 Jun 1894, 2,400 m, *M. E. Jones 5440* (US).

STATUS: Endemic, rare and local; threatened (Ripley, T).

DISTRIBUTION: Iron (UT), Sevier, and Utah counties, Utah (BRY; Keck 1937a).

Penstemon acaulis L. O. Williams, Ann. Missouri Bot. Gard. 21: 345. 1934.

STATUS: Restricted, rare and threatened (Ripley, T).

DISTRIBUTION: Daggett Co., Utah (NY, US, UTC) and adjacent Sweetwater Co., Wyoming (Keck 1937a).

Penstemon atwoodii Welsh, Great Basin Nat. 35: 378. 1976.

TYPE: South end of Horse Mtn., ca 10 miles south-southeast of Canaan Peak, Kane Co., Utah, 14 Jun 1975, *S. L. & S. L. Welsh 12820* (BRY).

STATUS: Endemic, local and threatened.

DISTRIBUTION: Garfield and Kane counties, Utah (BRY, NY).

Penstemon bracteatus Keck, Leafl. W. Bot. 1: 82. 1934.

TYPE: Red Canyon, Garfield Co., Utah, 20 Jun 1933, *Eastwood & Howell 783* (CAS).

STATUS: Endemic, restricted and rare; possibly threatened.

DISTRIBUTION: Garfield Co., Utah (BRY).

Penstemon caespitosus Nutt. var. *suffruticosus* A. Gray, Syn. Fl. N. Amer. 2: 270. 1878.

TYPE: Near Beaver, Beaver Co., Utah, 1877, *Palmer s.n.* (GH).

STATUS: Endemic, restricted and local; threatened (Ripley, T).

DISTRIBUTION: Beaver, Garfield and Piute counties, Utah (Keck 1937a).

Penstemon compactus (Keck) Crosswhite, Amer. Midl. Naturalist 77: 6. 1967, based on *P. cyananthus* ssp. *compactus* Keck, Amer. Midl. Naturalist 23: 615. 1940.

TYPE: Stony slopes of Mt. Naomi, Cache Co., Utah, 18 Aug 1938, 2,900 meters, *Maguire 16148* (UTC).

STATUS: Endemic, restricted and threatened (Ripley, T).

DISTRIBUTION: Cache Co., Utah (BRY, UTC, WSCO).

Penstemon concinnus Keck, Amer. Midl. Naturalist 23: 608. 1940.

TYPE: Tunnel Springs, northwest corner of Desert Range Experiment Station boundary, about 10 miles east of Garrison, Millard Co., Utah, 28 Jun 1933, 1,675 meters, *Cottam 5635* (DS).

STATUS: Endemic, restricted and rare; endangered (Ripley, E).

DISTRIBUTION: Beaver and Millard counties, Utah (BRY, NY, US, UTC).

Penstemon garrettii Pennell, Contr. U.S. Natl. Herb. 20: 353. 1920.

TYPE: Crevices in travertine rock, "Hot Pots," near Midway, Wasatch Co., Utah, 6 Jul 1905, *Carleton & Garrett 6697* (NY).

STATUS: Endemic, restricted and possibly extinct.

DISTRIBUTION: Duchesne (UT) and Wasatch counties, Utah.

Penstemon grahamii Keck in Graham, Ann. Carnegie Mus. 26: 331. 1937.

TYPE: Talus slope on the west side of Green River, south of the mouth of Sand Wash, Uintah Co., Utah, 27 May 1933, *Graham 7883* (CM).

STATUS: Endemic, rare, restricted and endangered (Ripley, E).

DISTRIBUTION: Uintah Co., Utah (BRY, UTC; Keck 1938a).

Penstemon humilis Nutt. ex Gray var. *brevifolius* A. Gray, Syn. Fl. N. Amer. 2: 267. 1878.

TYPE: Cottonwood Canyon, Wasatch Mts., Salt Lake Co., Utah, 1869, 9,000-10,000 feet, *Watson 781* (GH).

STATUS: Endemic, local and possibly threatened.

DISTRIBUTION: Cache, Juab, Salt Lake, Utah, and Weber counties, Utah (BRY, UT).

Penstemon humilis Nutt. ex Gray var. *obtusifolius* (Pennell) Reveal, stat. nov., based on *P. obtusifolius* Pennell, Contr. U.S. Natl. Herb. 20: 370. 1920.

TYPE: Springdale, Washington Co., Utah, 16 May 1894, 1,600 meters, *M. E. Jones 5249am* (POM).

STATUS: Endemic, rare and restricted; possibly threatened.

DISTRIBUTION: Beaver and Washington counties, Utah (Keck 1945).

Penstemon jonesii Pennell, Contr. U.S. Natl. Herb. 20: 338. 1920.

TYPE: Springdale, Washington Co., Utah, 17 May 1894, *M. E. Jones 5250*, in part (US).

STATUS: Endemic, rare and obscure; taxonomic status questionable.

DISTRIBUTION: Washington Co., Utah; known only from the type locality.

Penstemon laevis Pennell, Contr. U.S. Natl. Herb. 20: 347. 1920.

Type: Red sand at Springdale, Washington Co., Utah, 17 May 1894, 1,200 meters, *M. E. Jones 5250*, in part (US).

Status: Endemic, restricted and local.

Distribution: Kane, Garfield, and Washington counties, Utah (BRY, UTC).

Penstemon leiophyllus Pennell, Contr. U.S. Natl. Herb. 20: 346. 1920.

Type: Mammoth Creek, Garfield Co., Utah, 10 Sep 1894, 2,400 meters, *M. E. Jones 6026b* (US).

Status: Endemic, restricted and local; threatened (Ripley, T).

Distribution: Garfield, Iron, Kane, and Washington counties, Utah (BRY).

Penstemon lentus Pennell var. *albiflorus* (Keck) Reveal, stat. nov., based on *P. lentus* ssp. *albiflorus* Keck, Amer. Midl. Naturalist 23: 616. 1940.

Type: Abajo Mts., ca 8 miles west of Blanding, near the "Bear's Ears," San Juan Co., Utah, 9 Jun 1938, 2,400 meters, *C. L. Porter 1801* (RM).

Status: Endemic, locally common and not threatened.

Distribution: San Juan Co., Utah (BRY).

Penstemon leonardii Rydb., Bull. Torrey Bot. Club 40: 483. 1913.

Type: Diehl's Grove, Wasatch Mts., possibly Utah Co., Utah, 1 Aug 1884, *Leonard s.n.* (NY).

Status: Endemic, locally common and not threatened nor endangered.

Distribution: Cache, Davis, Rich, Salt Lake, Summit, Uintah, Utah, Wasatch, Washington, and Weber counties, Utah (BRY, UT).

Penstemon longiflorus (Pennell) S. L. Clark, Great Basin Nat. 35: 434. 1976, based on *P. cyananthus* ssp. *longiflorus* Pennell, Contr. U.S. Natl. Herb. 20: 353. 1920.

Type: Beaver, Beaver Co., Utah, *Palmer 376* (NY).

Status: Endemic, restricted but locally common.

Distribution: Beaver, Millard, and Piute counties, Utah (BRY).

Penstemon nanus Keck, Amer. Midl. Naturalist 23: 607. 1940.

Type: Desert Range Experiment Station, about 10 miles east of Garrison, Millard Co., Utah, 13 May 1939, 1,675 meters, *Plummer 7313* (DS).

Status: Endemic, restricted and local; threatened (Ripley, E).

Distribution: Beaver and Millard counties, Utah (BRY, UTC).

Penstemon parvus Pennell, Contr. U.S. Natl. Herb. 20: 345. 1920.

Type: The Button, Aquarius Plateau, Wayne Co., Utah, 11 Aug 1875, *Ward 546* (US).

Status: Endemic, restricted and rare; threatened (Ripley, T).

Distribution: Garfield and Wayne counties, Utah, (BRY; Pennell 1920).

Penstemon sepalulus Rydb., Bull. Torrey Bot. Club 36: 690. 1909.

Type: Canyons of the Wasatch Mts., Provo Canyon, Utah Co., Utah, Jul 1869, *Watson 786* (NY).

Status: Endemic, locally abundant.

Distribution: Utah Co., Utah (BRY; Keck 1932).

Penstemon tidestromii Pennell, Contr. U.S. Natl. Herb. 20: 379. 1920.

Type: "XL" Canyon, San Pitch Mts., Sanpete Co., Utah, 24 Jun 1908, 1,650 meters, *Tidestrom 1296* (US).

Status: Endemic, local and obscure; taxonomic status questionable.

Distribution: Sanpete Co., Utah; known only from the type locality.

Penstemon uintahensis Pennell, Contr. U.S. Natl. Herb. 20: 350. 1920.

Type: Dyer Mine, Uinta Mts., Uintah Co., Utah, 30 Jun 1902, *Goodding 1221* (NY).

Status: Endemic, rare and restricted; threatened (Ripley, T).

Distribution: Daggett, Duchesne, and Uintah counties, Utah (BRY).

Penstemon wardii A. Gray, Proc. Amer. Acad. Arts 12: 82. 1876.

Type: Near Glenwood, Sevier Co., Utah, 4 Jun 1875, *Ward 162* (US).

Status: Endemic, restricted and local; threatened (Ripley, T).

Distribution: Sanpete and Sevier counties, Utah (BRY, UTC).

Synthris laciniata (A. Gray) Rydb. ssp. *ibapahensis* Pennell, Proc. Acad. Nat. Sci. Philadelphia 85: 92. 1933.

Type: Wet gravelly slopes near ravine of snow on Mount Ibapah, Juab

Co., Utah, 5 Jul 1932, 9,500-10,000 feet, *Stanton 1000* (PH).

STATUS: Endemic, restricted and obscure; taxonomic status questionable.

DISTRIBUTION: Juab Co., Utah; known only from the type locality.

SELAGINELLACEAE

Selaginella utahensis Flowers, Amer. Fern J. 39: 83. 1949.

TYPE: South of St. George, Washington Co., in a wash bottom, 5 Apr 1931, *Cottam 5644* (UT).

STATUS: Rare and local; possibly threatened.

DISTRIBUTION: Washington Co., Utah, and Spring Mts., Clark Co., Nevada (Cronquist et al. 1972).

VERBENACEAE

Aloysia wrightii (A. Gray) A. A. Heller, Muhlenbergia 1: 147. 1906, based on *Lippa wrightii* A. Gray, Amer. J. Sci. II, 16: 98. 1853.

STATUS: Local and rare; possibly endangered.

DISTRIBUTION: Washington Co., Utah (*Higgins 615* [BRY]; Higgins 1972b); from Texas to California and in northern Mexico.

VIOLACEAE

Viola purpurea Kellogg var. *charlestonensis* (Baker & Clausen) Welsh & Reveal, stat. & comb. nov., based on *V. charlestonensis* Baker & Clausen in Clokey, Madroño 8: 58. 1945.

STATUS: Restricted, local and rare; threatened (Ripley, T).

DISTRIBUTION: Washington Co., Utah, and Clark Co., Nevada (Clokey 1945; Eastmond 1969).

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[11] The abbreviation cited throughout this paper for this publication should be "Great Basin Naturalist" according to Lawrence et al. (1968) and not "Great Basin Nat." This is the only abbreviation cited in the paper that does not conform with standardized list.

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UTAH PLANT NOVELTIES IN *CYMOPTERUS* AND *PENSTEMON*

Stanley L. Welsh[1]

Abstract.— *Cymopterus higginsii* and *Penstemon atwoodii* are named and described from materials collected in the Kaiparowits Plateau vicinity of eastern Kane County, Utah. Habitat, distribution, and probable affinities are outlined.

Examination of specimens obtained from the Kaiparowits Plateau region of eastern Garfield and Kane counties in southern Utah has revealed the existence of two previously undescribed entities, one each in *Cymopterus* (Apiaceae) and *Penstemon* (Scrophulariaceae). Existence of these taxa is not surprising when one considers the historic remoteness of much of that great region. The discovery and the extent of the range of each taxon must be credited to the extensive fieldwork allowed under the baseline studies of the Navajo-Kaiparowits environmental project directed by personnel from Brigham Young University (Welsh, Murdock, and Wood 1975).

The *Cymopterus* species is known from saline soils of the Tropic Shale formation and associated pedimental gravels on fans and bajadas below the Straight Cliffs formation in that portion of Kane County from the Paria River eastward to the Last Chance Creek vicinity. Apparent relationships of *C. higginsii* seem to lie with *C. fendleri* from which it differs inter alia in the rose to purple flowers with evident pedicels and wider wings on the fruit. The pseudoscape is poorly developed.

The corollas in the *Penstemon* species are glandular hairy externally, and the taxon seems to belong with those species treated by Pennell (1920) as Section Cristati and by Keck (1938) illegitimately as Section Aurator. The nearest ally appears to be *P. jamesii* from which *P. atwoodii* differs as noted in the diagnosis. *P. atwoodii* is known only from middle elevations of the Kaiparowits region, where it grows on the Cretaceous formations in juniper-pinyon woodland.

Both species, the *Cymopterus* and the *Penstemon,* are plants of very restricted range. They are in areas which are now subject to commercial exploitation, and both should be considered as threatened species.

Cymopterus higginsii Welsh sp. nov.

Plantae acaulescentes non caespitosae pseudoscapis non vel non nisi evolutis infermis, pubescentes parse pili complanti: folia ovata vel subelliptica in circumscriptem, laminis 1.8-7.7 cm longis 1.5-6.0 cm latis bi- vel tripinnatis viridibus foliolosis longior quam latis pinnatis ad bipinnata, lobi obtusi ad rotundatos vel acutos raro, petiolis 1.8-14 cm longis; pedunculi folia longior ad extremum 2-12 cm longi, purpurascentes; involucrum vaginans margine scariosa; involucellum bracteolarum brevior quam floras, lobis aliquot dentatis acutis vel acuminatis; umbellae compactae, radiis 3-5, 1-10 mm longis, umbellula centrali sessili; pedicelli 1-6 mm longi; flores rosei ad purpurascens; fructus ovalis ad ellipticum 7-10 mm longus 5-8 mm latus, alis corpus subaequalis incrassatis spongiosis.

C. fendleri affinis sed floribus roseis ad purpurascens pedicellis evidentibus et alis corpus subaequalis.

Habitat and Distribution.— Tropic shale and pedimental covering derived from Straight Cliffs and other formations, on saline soils, from East Clark Bench eastward to Last Chance Canyon, at least 30 miles east of Glen Canyon City, eastern Kane County, Utah.

Type: Utah: Kane Co., Shadscale dominated bajada, on gravelly pedimental fan, east of None Butte, ca 17 miles east of Glen Canyon City, S. L. Welsh 12740, 31 May 1975 (Holotype BRY; Isotypes to be distributed). Paratypes: Utah: Kane Co., Site 9, Navajo-Kaiparowits Project, base of Smoky Mt., 2 miles from Ahlstrom Point junction, Atriplex-Kochia-

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Artemisia community, N. D. Atwood 3439, March 1972 (BRY); ca 2 miles north of Church Wells, on bench between Coyote Creek and Wahweap Creek, N. D. Atwood et al. 3493, 23 March 1972 (BRY); ca 30 miles east of Glen Canyon City, on Tropic Shale formation, N. D. Atwood 4549, 23 April 1973 (BRY).

The species is named to honor Larry Charles Higgins, student of Boraginaceae, especially of *Cryptantha,* and specialist in western botany generally.

Penstemon atwoodii Welsh sp. nov.

Herbae perennes 1.4-5.3 cm altae; caules pauci vel multi e caudicibus ramificantibus glabri infra medium pilis patulis glanduliferis super; folia glabra, basalia oblanceolata ad spathulata vel ovata ad elliptica raro integra 2.8-9.0 cm longa (0.2) 0.4-0.8 (1.4) cm lata, caulina lancilinearia ad oblonga vel spathulata, ± auriculata super integra vel serrata remota raro, 3.0-7.0 cm longa 0.3-0.8 (1.4) cm lata; inflorescentia verticillastorum distinctarum plurium; bracteae foliaceae; calyces 6.5-8.5 mm longi lobis lanceolatis herbaceis purpureis pilis glanduliferis; corollae pilis glanduliferis externis cyanae vel cyano-caesiae 13-16 mm longae expansae distales 5-6 mm latae glabrae intus praeter ad orficium labium inferum; antherarum thecae glabrae divaricatae vel explanatae; staminodium barbatum pilis luteo lineare; capsulae glabrae.

P. jamesii sensu lato affinis sed floribus parvioribus et glabris intus praeter ad orficium labium inferum.

Habitat and Distribution.— Kaiparowits, Wahweap, and Straight Cliffs formation at 6,200 to 8,000 feet elevation in pinyon-juniper woodland on the Kaiparowits Plateau of eastern Garfield and Kane counties, Utah.

Type: Utah: Kane Co., Gray sand of Kaiparowits formation, pinyon-juniper community, south end of Horse Mountain, ca 10 miles south-southeast of Canaan Peak, S. L. & S. L. Welsh 12820, 14 June 1975 (Holotype; BRY; Isotypes to be distributed).

Paratypes: Utah: Garfield Co., Death Ridge ca 16 miles southwest of Escalante, N. D. Atwood 5177, 30 May 1973; do S. L. Welsh & J. R. Murdock 12866, 28 June 1975. Kane Co., 4 miles southeast of summit of Collets Wash, Kaiparowits Plateau, N. D. Atwood s. n., 19 June 1969; Pinyon-juniper woods on basal Wahweap formation, ca 6 miles north of junction of Escalante road with head of Last Chance Creek, Kaiparowits Plateau, S. L. Welsh & J. R. Murdock 12793, 4 June 1975; do S. L. Welsh & J. R. Murdock 12973a, 4 June 1975.

This species is named to honor Nephi Duane Atwood, student of Hydrophyllaceae, field botanist extraordinary, and first to recognize the unique nature of this taxon.

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THE ZYGOPTERA (ODONATA) OF UTAH WITH NOTES ON THEIR BIOLOGY[1]

A. V. Provonsha[2]

Abstract.— Detailed distribution maps of Utah are provided for each of the 33 state species of Zygoptera. Notes on the general range, habitat preference, reproductive behavior, emergence data, and general biology of each species are also included.

As noted by Kormondy (1957), published data on the geographical distribution of western Odonata is scarce. Kennedy (1915) gave a partial list of the Odonata of Washington and Oregon, and in 1917 he published records from central California and Nevada. The Washington list has recently been updated by Paulson (1970) and a complete list and keys to the California Odonata is given by Smith and Pritchard (1956). Bick and Hornuff (1972) published many new Odonata records for northwestern Wyoming. Although Larsen (1952) and Musser (1962) added considerably to our knowledge of Utah Anisoptera, only one paper (Brown 1934) dealing exclusively with the Odonata of Utah included a treatment of the Zygoptera. Brown's report consisted of an annotated checklist including some 25 currently valid zygopteran species.

During the summers of 1970 and 1971 the state of Utah was extensively collected in an effort to gain an increased understanding of the distribution and species composition of the damselfly fauna of that area. Some 152 localities throughout the state were sampled, and the collections at the University of Utah, Utah State University, Brigham Young University, and Dixie College were examined. As a result, the list of Zygoptera known to occur in Utah has been expanded to 33. In addition, field work and rearing has added considerably to our knowledge of the biology of many species (also see Provonsha and McCafferty 1973).

No attempt has been made to cite in detail all collection records. Although county records may be adequate for some states where counties are numerous and relatively small, they are meaningless for Utah, where several counties contain over 5,000 square miles and in many cases more than one distinct biotic region. Instead, distributions based on all collecting localities known to the author are plotted for each species.[3] For those instances where counties are mentioned in the text, the reader may refer to Fig. 1 for their specific location. Where possible, notes on general distribution, habitat preferences, emergence data, and reproductive behavior are included in the text.

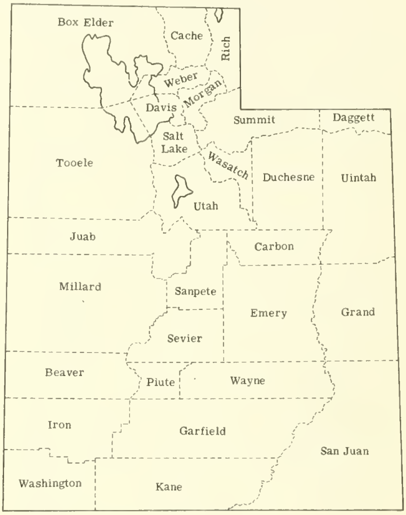

Fig. 1. County map of Utah.

For keys to the zygopteran species known to occur in Utah, the author recommends the following publications: Johnson (1972), Smith and Pritchard (1956), and Walker (1953).

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[3] Complete collecting data may be obtained from the author upon request.

[1] Published with the approval of the Director of the Purdue University Agricultural Experiment Station as Journal Series No. 6034.

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Calopteryx aequabilis Say, 1839
Fig. 2

This species is known to occur throughout most of Canada east of Saskatchewan and the north central and northeastern United States, with isolated pockets in Colorado, California, and the Columbia River drainage system. The major population of *C. aequibilis* in Utah is found at the Raft River, Box Elder Co., which is the only major river in Utah flowing north as part of the Columbia River drainage system. One other small isolated population occurs at Far West, Weber Co. A single male was collected at Goshen, Utah Co., on 19 May 1969, by P. V. Winger. Subsequent collections at that locality have failed to provide additional specimens, and it is doubtful that a population is established there. The species is restricted to streams where the nymphs cling to debris and submerged roots along the banks. The above record from Goshen is the earliest Utah record I have; species have been taken at the Raft River through mid-September. This species does not oviposit in tandem; however, the male remains in close proximity to the female and actively wards off other intruding males. Martin (1939) and Walker (1953) observed females descending as much as one foot below the water to deposit eggs. In July 1971 I observed several females ovipositing at the Raft River. On this occasion none submerged but completed oviposition just below the water line in algal mats in shallow water close to the bank. It must be noted, however, that the water level was lower than usual and there was little suitable vegetation in the deeper portions of the river.

Hetaerina americana (Fabricius, 1788)
Fig. 2

With the exception of the far eastern and northwestern states and Florida, *H. americana* has a general distribution throughout the United States and extends southward through Mexico into Guatemala. It is found throughout Utah in rivers and streams below 5,800 feet elevation which have a moderate flow and sufficient marginal vegetation for oviposition and nymphal development. The earliest emergence date I have for the state is 29 May. The nymphs emerge over most of the summer and can be found in the adult stage to the end of September. The female oviposits singularly and completely submerge to deposit their eggs, while the male, which perches nearby, faces the submerged female and actively fends off intruding males (Johnson 1961 and Bick and Sulzback 1966).

Hetaerina vulnerata Hagen, 1853
Fig. 2

H. vulnerata is restricted to the southwestern United States and Mexico, entering only the southwest corner of Utah in Washington County, which is part of the Mohave Desert Lower Sonoran. Like *H. americana*, the nymphs are found on roots, vegetation, and debris in streams with a moderate current. Although these two species were found at nearby streams, they were never taken at the same localities (Provonsha and McCafferty 1973).

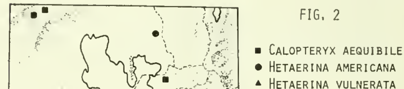


FIG. 2

Emergence begins around the first of June and is probably completed by mid-July. I am not aware of any reproductive studies conducted on this species, and I have never observed any in copulation. However, it is assumed that the method of oviposition is similar to that of *H. americana*.

Archelestes grandis (Rambur, 1842)

Fig. 3

Although this species ranges over much of the United States, in Utah it is restricted to the southern deserts. The nymphs are active swimmers and can be found in ponds and slow desert streams. All Utah collecting sites were below 4,600 feet. *A. grandis* is the largest of all Nearctic damselflies, the females having a wing span of approximately 40 mm. Like most other lestids, it is a late emerger. The earliest Utah record I have is 9 July. Bick and Bick (1970) reported that in Oklahoma emergence is much earlier and that oviposition is common by mid-June. In that area the eggs reportedly hatch approximately 16 days after oviposition, and the nymphs overwinter in a fairly late stage of development. However, there is some evidence that in the western deserts, where emergence tends to be later and where there is often a winter drought, eclosion may be delayed until the following spring. Oviposition takes place in tandem, and the eggs are deposited as high as 13 m above water in woody plants overhanging the water. This unique reproductive behavior has enabled this species to colonize certain habitats, such as desert streams, where marginal vegetation may be plentiful but vegetation within the water may be wanting.

Lestes congener Hagen, 1861

Fig. 3

This species is found over much of the United States and is by far the most common and wide-ranging *Lestes* in Utah. All collecting sites were at permanent and semipermanent ponds or "pondlike" expansions of slow streams at altitudes ranging from 4,200 to 7,000 feet. The nymphs are free swimmers and seem to prefer shallow ponds with some areas free of vegetation. Emergence begins in early July and continues through late August. As in most other *Lestes* species, the eggs are usually deposited some distance above water. However, on one occasion during flood conditions I observed two females submerge their abdomens almost to the base to deposit eggs below the water line.

Lestes disjunctus disjunctus Selys, 1862

Fig. 4

Although primarily found in Canada, Alaska, and the northern regions of the United States, this species does follow the mountains south through Utah and Colorado into Arizona. In Utah it was found mainly at permanent and semipermanent, richly vegetated ponds in mountainous areas between 5,000 and 7,000 feet. Emergence begins around mid-July and continues through mid-August. Although ovi-

FIG. 3

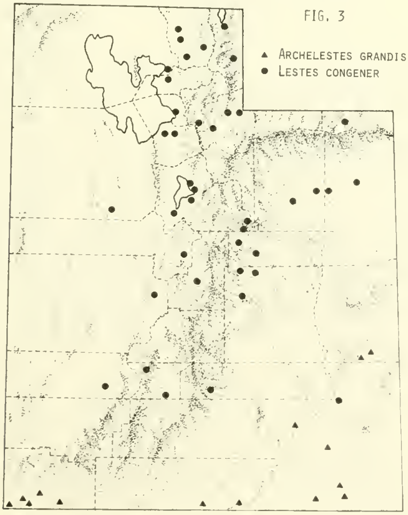
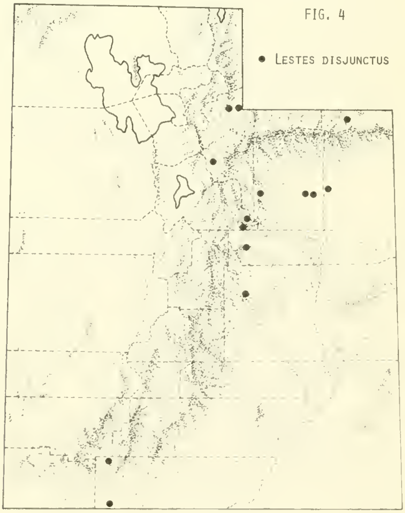


FIG. 4



position usually takes place well above water, on two separate occasions in 1970 I observed paired adults completely submerge to ovipost. These observations were made during flood conditions when more than the usual amount of vertical stems were below water. These observations coincide for the most part with observations by Bick and Bick (1961) for *L. d. australis* Walker.

Lestes dryas Kirby, 1890

Fig. 5

This species is Holarctic, occurring not only in North America but Europe and Asia as well. It is found most commonly at permanent and semipermanent ponds and less frequently in marshy areas. It was the only *Lestes* species taken above 8,000 feet in Utah. Although the locality records are scattered, *L. dryas* tended to be the dominant species at these localities. Emergence begins about the last week in June and continues through mid-August.

Lestes unquiculatus Hagen, 1861

Fig. 6

The range of *L. unquiculatus* is transcontinental in the northern United States and southern Canada. It was found at only a few localities in Utah and never in any large numbers. Specimens were collected primarily at temporary and semipermanent marshy areas between 5,000 and 6,350 feet. Emergence data for the state is insufficient. However, Walker (1953) reported that in Canada they fly mainly in July and August.

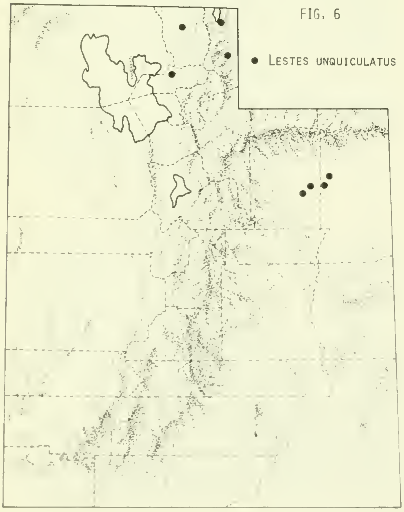


FIG. 6

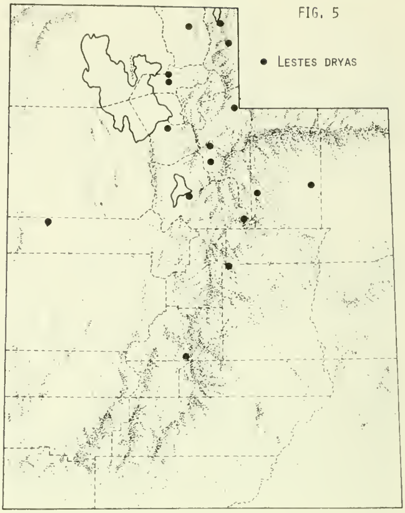


FIG. 5

Argia alberta Kennedy, 1918

Fig. 7

A. alberta is restricted to the western United States. Although it occurs in most regions of Utah at altitudes between 4,000 and 6,500 feet, it was never taken in any large numbers. The nymph has not been described, and none were taken during this study. With the exception of the San Juan River in San Juan Co., all adults were taken in association with small, slow flowing streams or marshy springs. The earliest collecting record I have for the state is 4 June and the flight period extends through the end of August. As with most *Argia* species, oviposition usually takes place in tandem.

Argia emma Kennedy, 1915

Fig. 8

This species is found in the western United States and British Columbia. In Utah it is found in the mountainous areas

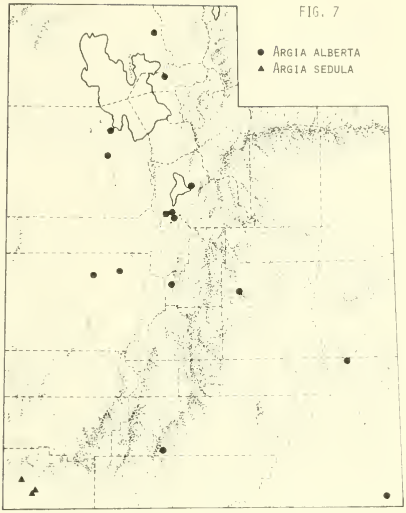


FIG. 7

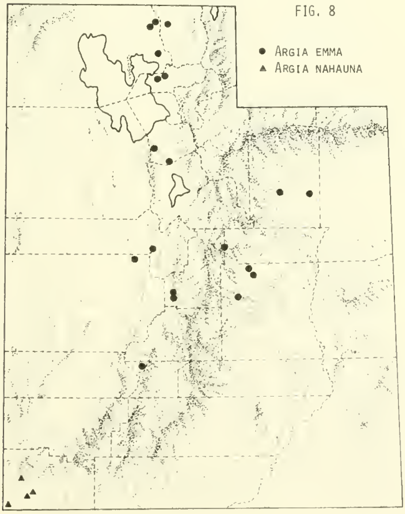


FIG. 8

in the northern two-thirds of the state in rivers and streams with gentle to moderate currents at altitudes between 4,200 and 5,800 feet. The nymphs may be found on stones but were most frequently taken on roots and debris near the bank. Emergence begins around the first of June and continues through mid-July and oviposition usually takes place in tandem.

Argia fumipennis violacea (Hagen, 1861)

This species is known from Guatemala north through the southwestern United States, most of the central and eastern United States, and eastern Canada. However, I have seen only one specimen from Utah (Univ. of Mich. Coll.). The label read: "Utah E. M. Legard #55." Although specific local information was lacking, it is speculated, based on overall distribution, that this specimen was collected in the Lower Sonoran region of Washington Co. It is reported that *A. f. violacea* prefers small lakes and shallow streams with moderate currents and exposed rocks (Walker 1953).

Argia lugens (Selys, 1854)

Fig. 9

This species is found only in Mexico and the southwestern United States. The only Utah records I have are from Zion National Park and Leeds Canyon (both in Washington Co.) where the nymphs inhabit permanent desert streams. I have no emergence data for the state. All specimens examined were collected during the month of July.

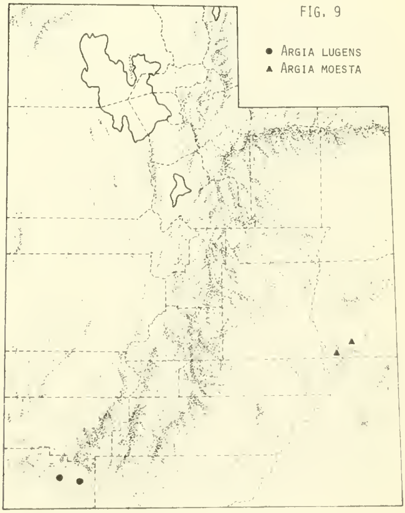


FIG. 9

Argia moesta (Hagen, 1861)

Fig. 9

Although common throughout North America with the exception of the northwestern states and western Canada, this species has been taken in Utah only from the Colorado River, where the nymphs can be found on rubble and in debris near the bank. Emergence begins in late May and continues through most of June. Walker (1953) reports that females oviposit either in tandem or unattended by the male and that they may completely submerge to deposit their eggs. Unlike most western species of *Argia*, which prefer to light on bare ground, all individuals of *A. moesta* observed in Utah rested on willows along the river's edge.

Argia nahauna Calvert, 1901

Fig. 8

This species is known only from the southwestern United States, entering Utah only in Washington Co. It is found at small streams with moderate currents and occasionally in permanent desert springs. At most localities it was found in association with *A. sedula*. The earliest Utah record I have is 5 June and the latest is 9 September.

Argia sedula (Hagen, 1861)

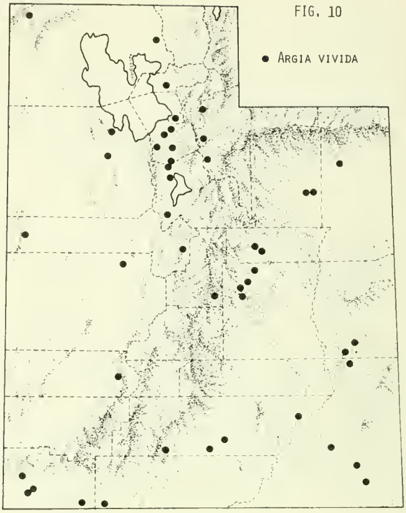
Fig. 7

The reported range of *A. sedula* includes most of the southern portion of the United States, northern Mexico, the midwestern states, and southern Ontario. In Utah it was found only in Washington Co. at altitudes between 2,800 and 4,400 feet. The nymphs prefer small streams with gentle current and a rich growth of vegetation. Emergence begins in mid-May and continues through mid-June.

Argia vivida Hagen, 1865

Fig. 10

FIG. 10



A. vivida is restricted to the western United States and southwestern Canada. It is fairly common in Utah and can be found at most rivers and streams with moderate currents. During this study they were taken at altitudes between 2,800 and 6,500 feet. Although they can be found in debris along the stream banks, the nymphs prefer stones and rubble well within the main current of the stream. Emergence begins around the first of June and continues through mid-July. Oviposition takes place in tandem, and eggs are laid just below the water surface in a wide variety of aquatic plants. Like most other *Argia* species, the males will frequently balance in a vertical position during oviposition when the immediate environment does not provide a good object for them to grasp.

Amphiagrion abbreviatum (Selys, 1876)

Fig. 11

This species is known from the western United States and southwestern Canada. I found this species at a great many localities throughout the state, but never in any large numbers. The habitats were varied, ranging from moderately flowing streams with gravel bottoms, to heavily vegetated ponds and springs, to large lakes. However, as Whitehouse (1941) found, they tend to prefer shallow, sunlit marshy areas with little or no current. They were taken at altitudes between 4,200 and 7,500 feet. Emergence begins in early May and the flight period extends through the end of August. Oviposition usually takes place in tandem, but I have observed unattended females probing algal mats.

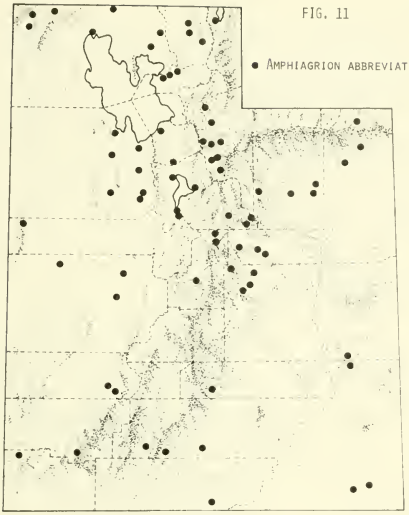


FIG. 11

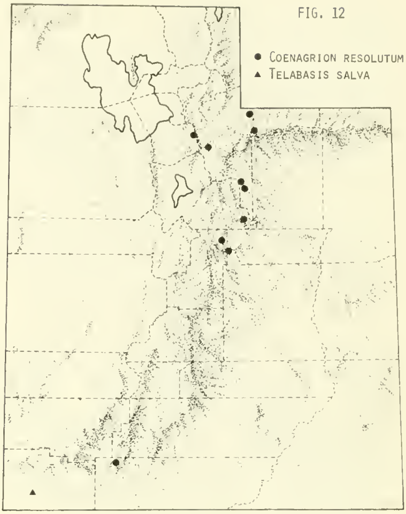


FIG. 12

Telebasis salva (Hagen, 1861)
Fig. 12

T. salva ranges from the southwestern United States to Venezuela. I have seen only three specimens taken in Utah. They were all collected at a small spring-fed pond near St. George, Washington Co.: two in 1941 (Univ. of Utah Coll.) and one in 1959 (Dixie College Coll.). Recently the area has been converted into a golf course, greatly changing the original habitat. It is possible that this species no longer occurs in the state.

Coenagrion resolutum (Hagen, 1876)
Fig. 12

This species is known from throughout most of Canada and Alaska, the northeastern states, and higher elevations in the West. In Utah it was found at small ponds and slow-flowing high meadow streams above 7,000 feet, where they emerge during the month of July. Evidently all oviposition is in tandem.

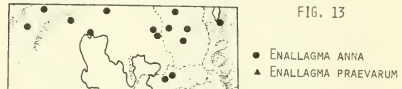


FIG. 13

Enallagma anna Williamson, 1900
Fig. 13

E. anna is restricted to the western United States. This species is fairly common throughout the mountainous areas of northern Utah at altitudes between 4,200 and 7,000 feet. Nymphal development takes place in rivers and streams with slow to moderate currents. The flight period ranges from mid-May through the first of September, and, like most other species of *Enallagma*, oviposition takes place in tandem.

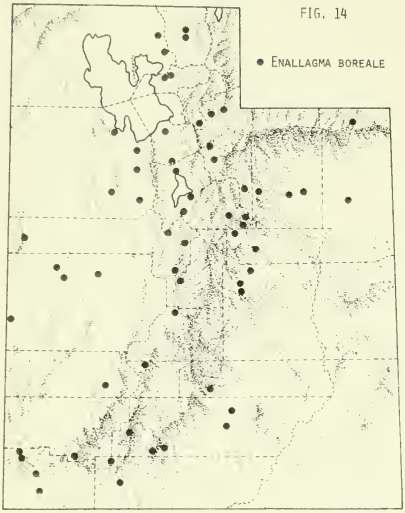


FIG. 14

Enallagma boreale Selys, 1875
Fig. 14

The range of this species includes most of Canada and the northern United States with isolated populations at higher altitudes in the southwest. Next to *Ischnura perparva* Selys, it is the most common species in Utah, being absent only from the desert areas in the southeast. It is most frequently found at lakes and ponds and rarely at slow-flowing streams. Collection sites ranged from 4,000 to 9,000 feet. It is an early emerger, and the first record I have for the state is 8 May. None were taken after mid-August. Oviposition usually takes place in tandem.

Enallagma carunculatum Morse, 1895
Fig. 15

With the exception of a break along the Rocky Mountains, this species is found transcontinentally in southern Canada and the northern United States, extending southward in the West into northern Mexico. This is one of the more common and widely adapted species in Utah, often occurring in great numbers. Although it was most frequently found at small ponds, it was also taken at streams, rivers, and some of the larger lakes and reservoirs at altitudes between 3,000 and 8,000 feet.

E. carunculatum is one of the few species which can develop in brackish water, such as that occurring in drainage ditches west of Salt Lake City near the Great Salt Lake, where it was found in close association with *E. clausum* Morse. This association has also been reported for other brackish waters such as Pyramid Lake, Nevada (Kennedy 1917). Emergence begins in late May, and oviposition takes place in tandem.

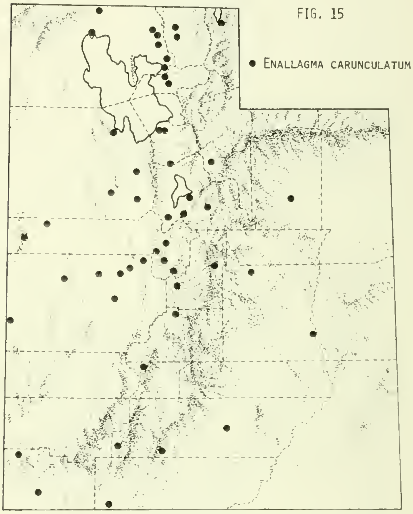


FIG. 15

Enallagma civile (Hagen, 1861)
Fig. 16

With the exception of the far northwest, *E. civile* has a wide range over most of the United States and extends as far south as the West Indies and Colombia. Although this is one of the most common species in North America, it was taken at only a few scattered localities in Utah. Locally abundant populations were taken in the Sevier River drainage system in Millard Co., but only small numbers were taken at most other collecting sites. Nymphs were taken in lakes, ponds, and streams and rivers with slow currents at altitudes from 2,800 to 6,000 feet. Like its close relative *E. carunculatum*, emergence begins in late May and continues through most of the summer.

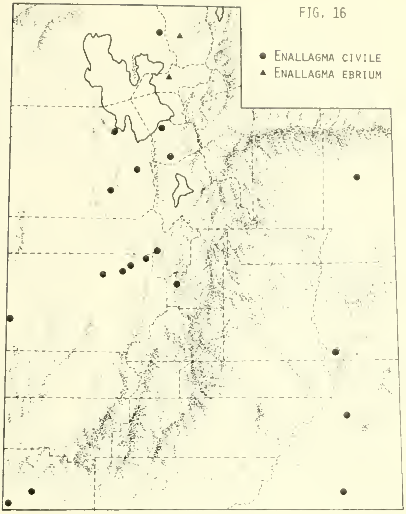


FIG. 16

Enallagma clausum Morse, 1895

Fig. 17

This species is found in the western United States and southwestern Canada with isolated populations in Ontario and Quebec. In Utah it is restricted to the western half of the state at altitudes between 4,200 and 6,300 feet. The nymphs may be found in slow streams and lakes with some wave action. *Enallagma clausum* is tolerant to saline conditions and was frequently found in association with *E. carunculatum* at brackish waters in the western desert. Unlike most species of *Enallagma*, adults prefer to rest on bare ground rather than on vegetation; when they are at rest the wings are frequently held at a slight angle away from the body. Emergence begins in late May and continues through most of the summer.

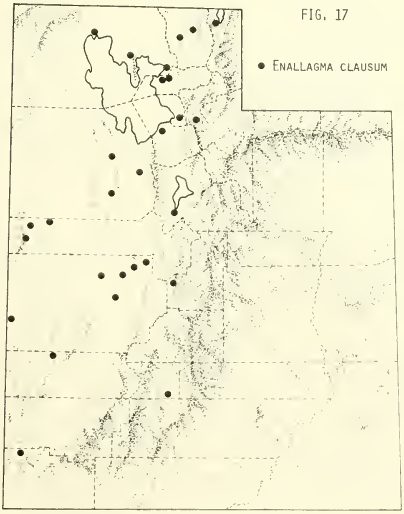


FIG. 17

Enallagma cyathigerum (Charpentier, 1840)

Fig. 18

This is a Holarctic species, being found in Europe, Asia, Canada, and most of the northern United States. It is one of the more common species in Utah and is absent only from the western deserts. Although most common at small ponds, it was frequently taken at streams with slow to moderate currents. With the exception of *Coenagrion resolutum*, it was the only species taken above 9,000 feet. Emergence begins in mid-June, and adults can be found through early September.

Enallagma ebrium (Hagen, 1861)

Fig. 16

The range of this species is reported as Boreal North America. It has been taken at only two localities in Utah. Fourteen specimens were collected at the Weber River, West Weber, Weber Co., by C. J. D. Brown (1934), and two adults were collected during this present study at marshy areas along the Bear River in Cache Co. Both of the above-mentioned collections were made in July. Walker (1953) records the flight period in Canada to be from 30 May through 24 August.

Enallagma praevarum (Hagen, 1861)

Fig. 13

This species ranges from the southern United States to southern Mexico. In Utah it is restricted to desert streams and springs at 2,800 to 5,800 feet elevation in the unique southwest corner of the state. Although very closely related to *E. anna*, at no place did their ranges overlap. Emergence begins in mid-May and continues through the month of June.

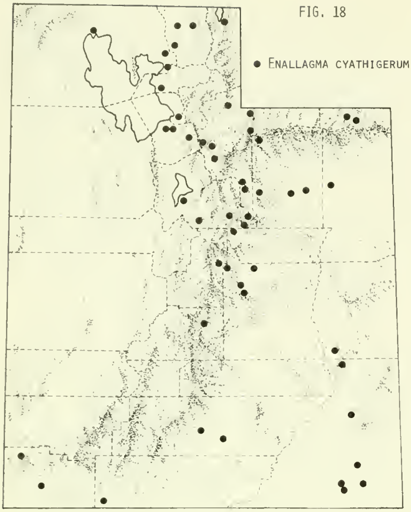


FIG. 18

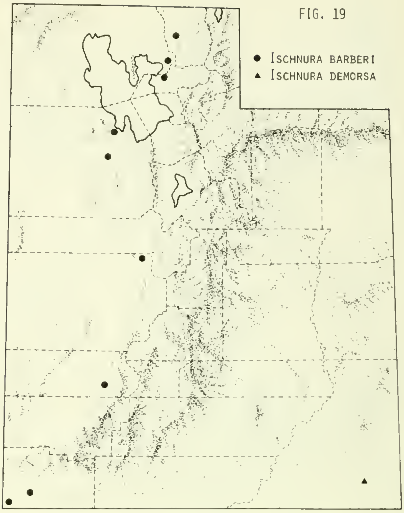


FIG. 19

Ischnura barberi Currie, 1903
Fig. 19

Ischnura barberi is known only from the western United States. All collecting sites in Utah were at ponds in the western portion of the state at altitudes ranging from 2,800 to 4,730 feet. This species appears to be rare in numbers, since no more than two specimens were taken at any one locality. Oviposition was never observed. All collections were made during the months of June and July.

Ischnura cervula Selys, 1876
Fig. 20

Southwestern Canada, western United States, and northern Mexico are included in the range of this species. It is fairly common and was frequently found at ponds and slow streams with a preference for shallow marshy areas. Samples were from altitudes ranging from 4,200 to 7,000 feet. Oviposition does not usually take place in tandem. Emergence begins in early May and continues through most of the summer.

Ischnura damula Calvert, 1901
Fig. 21

This species is known in southern Canada from Manitoba west and the western United States. Except for the warm springs in Tooele Co., its distribution in Utah is restricted to the southern portion of the state. All specimens were collected from small ponds and springs with dense stands of cattails along the margins. All sites were between an altitude of 4,225 and 5,825 feet. Females were observed ovipos-

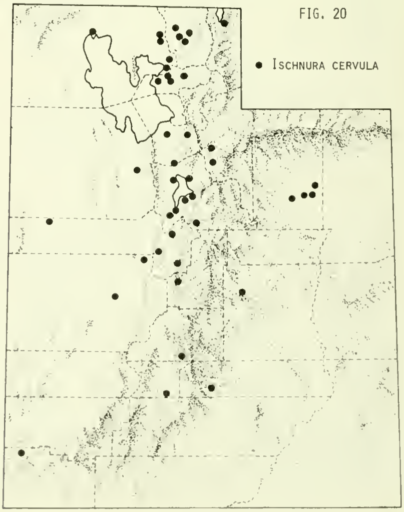


FIG. 20

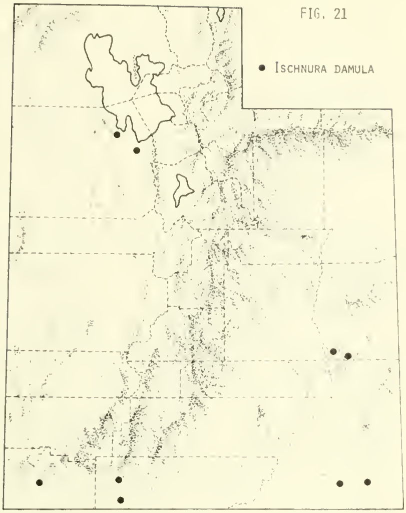


FIG. 21

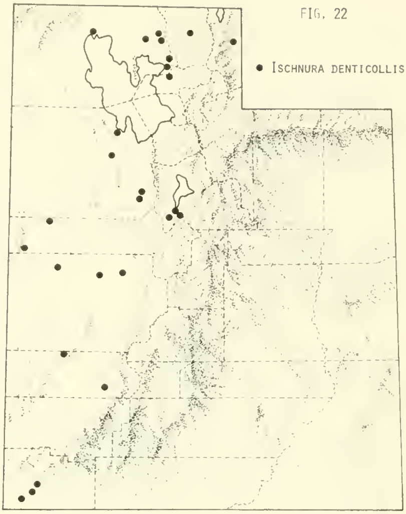


FIG. 22

iting singularly and in tandem. The earliest record I have for the state is 23 May. It is probable that emergence begins in early May and continues through early July.

Ischnura demorsa (Hagen, 1861)

Fig. 19

Ischnura demorsa is reported from the western United States and Mexico. This close relative of *I. perparva* is rare in Utah, however. Only two specimens were taken during this study, both from McCracken Spring in San Juan Co. at an altitude of 4,900 feet. I have no emergence data for this species.

Ischnura denticollis (Burmeister, 1839)

Fig. 22

This species is found only in the southwestern United States and Mexico. In Utah it is restricted to the cold deserts in the western half of the state. It is equally suited to both ponds and streams and is tolerant to a wide range of altitudes, being found from 2,700 to 6,300 feet. Oviposition usually takes place in tandem. This species tends to emerge somewhat later than most other Utah ischnurans. No specimens were taken before the first of June, and 15 August was the last date they were encountered.

Ischnura perparva Selys, 1876

Fig. 23

This species is known from the western United States and southwestern British Columbia. This is by far the most common damselfly in Utah. It was found at 87 of the 152 localities sampled during this

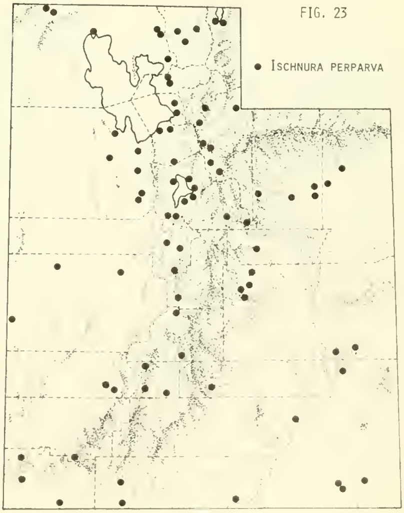


FIG. 23

study (almost twice as many as any other species). Its great abundance can be attributed, in part, to its ability to survive in many diverse habitats. It was found in most aquatic situations between 4,200 and 7,500 feet where there was sufficient vegetation and a high enough minimum temperature to support zygopteran forms. Although oviposition may take place in tandem, it is usually accomplished unattended by the male. Emergence begins in early May and continues throughout most of the summer.

Acknowledgments

The author wishes to thank Dr. George F. Edmunds, Jr., University of Utah; Dr. Wilford J. Hanson, Utah State University; Dr. Vasco M. Tanner, Brigham Young University; and Dr. Andrew H. Barnum, Dixie College, for the loan of specimens. Gratitude is also extended to Mrs. Leonora K. Gloyd, Museum of Zoology, University of Michigan, and Dr. Minter J. Westfall, Jr., University of Florida, for verification of identifications and advice given during this study. Special appreciation is expressed to Dr. W. P. McCafferty, Purdue University, for his encouragement, advice, and assistance both during the study and in the preparation of the manuscript.

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NEW SYNONYMY AND NEW SPECIES OF AMERICAN BARK BEETLES (COLEOPTERA: SCOLYTIDAE), PART II[1]

Stephen L. Wood[2]

ABSTRACT.— New synonymy is proposed as follows: *Pityophthorus* Eichhoff (= *Gnathophorus* Schedl, *Gnathophthorus* Wood), *Araptus confinis* (Blandford) (= *Neopityophthorus glabricollis* Schedl), *A. eruditus* (Schedl) (= *Neodryocoetes buscki* Blackman), *A. hymenaeae* (Eggers) (= *Neodryocoetes humilis* Blackman), *A. schedli* (Blackman) (= *Neodryocoetes lenis* Blackman), *A. tenellus* (Schedl) (= *Ctenyophthorus mexicanus* Schedl, *Neodryocoetes granulatus* Schedl, *Araptus cuspidus* Wood), *Coccotrypes carpophagus* (Hornung) (= *Coccotrypes liberiensis* Hopkins, *Coccotrypes punctatulus* Eggers), *C. dactyliperda* (Fabricius) (= *Coccotrypes bassiavorus* Hopkins), *C. robustus* Eichhoff (= *Coccotrypes cylindricus* Schedl), *Cryptocarenus heveae* (Hagedorn) (= *Cryptocarenus caraibicus* Eggers), *Hypothenemus setosus* (Eichhoff) (= *Stephanoderes congonus* Hagedorn), *Microcorthylus minutus* Schedl (= *Microcorthylus minutissimus* Schedl), *Pseudopityophthorus limbatus* Eggers (= *Pseudopityophthorus micans* Wood), *Xyleborus obliquus* (LeConte) (= *Xyleborus gilvipes* Blandford, *X. brasiliensis* Eggers, *illepidus* Schedl). *Hypothenemus javanus* Eggers is a valid species. The genus *Dacnophthorus*, type-species *Gnathophthorus clematus* Wood, is described as new to science. The following species are described as new to science: *Araptus consobrinus*, *A. micaceus*, *Pityophthorus explicitus*, and *P. inceptis* (Mexico), *P. costatus* and *P. mendosus* (Costa Rica), *P. degener* and *P. timidulus* (Panama), *P. amiculus* (Mexico, Costa Rica), and *P. dissolutus* (Costa Rica, Panama), *Xyleborus californicus* (California), *X. incultus*, *X. molestulus* (Panama), and *tristiculus* (Brazil).

On the following pages several newly discovered cases of synonymy, one new genus, and 14 species new to science are presented for American Scolytidae. The specific synonymy is presented alphabetically for convenience of reference. The species new to science represent the genera *Araptus* (2), *Pityophthorus* (8), and *Xyleborus* (4). They are from the following countries: United States (1), Mexico (4), Costa Rica (2), Panama (4), Brazil (1), Mexico and Costa Rica (1), Costa Rica and Panama (1).

NEW SYNONYMY

Pityophthorus Eichhoff

Pityophthorus Eichhoff, 1864, Berliner Ent. Zeit. 8:39 (Type-species: *Bostrichus lichtensteini* Ratzeburg, subsequent designation by Hopkins, 1914, Proc. U.S. Nat. Mus. 48:127)

Gnathophorus Schedl, 1935 (nec Kirby, 1837), Rev. de Ent. 5:342 (Type-species: *Gnathophorus sparsipilosus* Schedl, monobasic). *New synonymy*

Gnathophthorus Wood, 1962, Great Basin Nat. 22:76 (Replacement name for *Gnathophorus*). New synonymy

The holotype of *Gnathophorus sparsipilosus* Schedl was examined and compared directly to a series of this species in my collection. It fits well within the limits of the genus *Pityophthorus* anatomically as well as biologically. For this reason the names *Gnathophorus* and its replacement, *Gnathophthorus*, must be placed in synonymy as indicated above. The five species subsequently assigned to this genus must be transferred to another genus that is described below.

Araptus confinis (Blandford)

Pityophthorus confinis Blandford, 1904, Biol. Centr. Amer. Coleopt. 4(6):241 (Lectotype, male; Jalapa, Veracruz, Mexico; British Mus. Nat. Hist., present designation)

Neopityophthorus glabricollis Schedl, 1938, Archiv Naturgesch. 7(2):181 (Holotype, male; Teopisca, Chiapas, Mexico; Schedl Coll.). *New synonymy*

The first syntype in the type series of *Pityophthorus confinis* Blandford is here designated as the lectotype of that species. This lectotype was compared directly to my males from Guatemala City, Guatemala, and was found to be identical in all respects. My series was later compared directly to the male holotype of *Neopityophthorus glabricollis* Schedl. Except for the loss of declivital and frontal setae, an apparent result of abrasion on the Schedl type, these specimens are also identical. As indicated above, the junior name must be placed in synonymy. The lectotype of *confinis* is labeled "Type" and has been considered as the type for many years.

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[1] Part of this research was sponsored by the National Science Foundation.

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Araptus eruditus (Schedl)

Neopityophthorus eruditus Schedl. 1938, Archiv Naturgesch., n. f., 7(2):182 (Holotype, female; Mexico; Schedl Coll.)

Neodryocoetes buscki Blackman, 1942, Proc. U.S. Nat. Mus. 92:192 (Holotype. female; Cabima, Panama; U.S. Nat. Mus.). *New synonymy*

The female holotype of *Neopityophthorus eruditus* Schedl and the female holotype of *Neodryocoetes buscki* Blackman were compared directly to my series. All represent the same species. The last visible abdominal sternum is armed by a subtuberculate callus which aids in the identification of this species.

Araptus hymenaeae (Eggers)

Neodryocoetes hymenaeae Eggers, 1933, Mem. Trav. Lab. d'Ent. Mus. Nat. d'Hist. Nat., Paris 1(1):9 (Holotype, female; Gourdonville, French Guiana; Paris Mus.)

Neodryocoetes humilis Blackman, 1942, Proc. U.S. Nat. Mus. 92:188 (Holotype, female; Bonito, Pernambuco, Brazil; U.S. Nat. Mus.) *New synonymy*

The variable frons of this species has led to the description of several synonyms. Following a study of the holotype and six cotypes of *Neodryocoetes hymenaeae* Eggers, the female holotype of *Neodryocoetes humilis* Blackman, and 76 other specimens, it was concluded that only one species was represented and that Blackman's name must be placed in synonymy.

Araptus schedli (Blackman)

Neodryocoetes schedli Blackman, 1942, Proc. U.S. Nat. Mus. 92:195 (Holotype, male; Tampico, Mexico; U.S. Nat. Mus.)

Neodryocoetes lenis Blackman, 1942, Proc. U.S. Nat. Mus. 92:198 (Holotype, male; Cordoba, Veracruz. Mexico; U.S. Nat. Mus.). *New synonymy*

The male holotypes of *Neodryocoetes schedli* Blackman and *Neodryocoetes lenis* Blackman were compared directly to one another and to several specimens intercepted at New York in seeds of Mexican origin. I am unable to detect any differences among these specimens that might justify the continued recognition of two names.

Araptus tenellus (Schedl)

Neodryocoetes tenellus Schedl, 1951, Dusenia 2: 109 (Holotype, male; Chiapas, Mexico; Schedl Coll.)

Ctenyophthorus mexicanus Schedl, 1963, Ent. Arb. Mus. Frey 14:162 (Holotype, female; Trampaluz, Escarcaga, Campeche, Mexico; Schedl Coll.). *New synonymy*

Neodryocoetes granulatus Schedl, 1964, Reichenbachia 3:311 (Replacement name for *Ctenyophthorus mexicanus* Schedl). *New synonymy*

Araptus cuspidus Wood, 1974, Brigham Young Univ. Sci. Bull., Biol. Ser. 19 (1):46 (Holotype, female; 8 km E San Blas, Nayarit, Mexico; Wood Coll.). *New synonymy*

The holotype of *Neodryocoetes tenellus* Schedl and the allotype of *Araptus cuspidus* Wood were compared directly to one another. Except for minor differences in the convexity of the frons, they are identical. The peculiar abdominal sternum 5 was not mentioned by Schedl. The Schedl holotype of *Ctenyophthorus mexicanus* is a female, not a male as stated in the original description. It was compared directly to the holotype of *cuspidus* and was found to be identical. The two junior names and the replacement name, *Neodryocoetes granulatus* Schedl, must be placed in synonymy as indicated above.

Coccotrypes carpophagus (Hornung)

Bostrichus carpophagus Hornung, 1842, Stettiner Ent. Zeit. 3:116 (Syntypes; intercepted in Germany from "Betelnüssen" of "Ostindien" origin)

Coccotrypes liberiensis Hopkins, 1915, U.S. Dept. Agric. Rept. 99:47 (Holotype, female; Mount Coffee, Liberia; U.S. Nat. Mus.). *New synonymy*

Coccotrypes punctatulus Eggers, 1951, Ent. Blätt. 45-46:151 (Holotype, female; Insel St. Thomas, Virgin Islands; deposited in Eggers Coll., apparently on loan to Schedl). *New synonymy*

The holotypes of *Coccotrypes liberiensis* Hopkins and *C. punctatulus* Eggers and the syntypes of *Bostrichus carpophagus* Hornung were all examined and compared directly to my series of this species. Only one species is represented by the three names.

Coccotrypes dactyliperda (Fabricius)

Bostrichus dactyliperda Fabricius, 1801, Systema Eleutheratorium 2:387 (Syntypes; in date pits intercepted in Europe; Copenhagen and Berlin museums)

Coccotrypes bassiavorus Hopkins. 1915, U.S. Dept. Agric. Rept. 99:47 (Holotype, female; Washington, D.C.; U.S. Nat. Mus.). *New synonymy*

Several female specimens of *Coccotrypes dactyliperda* (Fabricius) that were compared by Eggers to the Fabricius syntypes were compared directly to the female holotype of *C. bassiavorus* Hopkins. Since they are identical in all respects, Hopkins's name must be placed in synonymy.

Coccotrypes robustus Eichhoff

Coccotrypes robustus Eichhoff. 1878, Mém. Soc. Roy. Sci. Liége (2)8:313 (Syntypes?; Cuba; presumably lost with Hamburg Mus.)

Coccotrypes cylindricus Schedl, 1949, Tijdschr. Ent. 91:116 (Holotype, female; Crucos. Cuba; Schedl Coll.). *New synonymy*

A female of *Coccotrypes robustus* Eichhoff that was compared by Hopkins to a syntype and the holotype of *C. cylindricus* Schedl were compared to my series of this species. Since all represent the same distinctive species, Schedl's name must be placed in synonymy.

Cryptocarenus heveae (Hagedorn)

Stephanoderes heveae Hagedorn, 1912, Rev. Zool. Afr. 1:338 (Syntypes, female; Eala, Congo; Tervuren Mus.)

Cryptocarenus caraibicus Eggers, 1937, Rev. de Ent. 7:82 (Holotype, female; Guadeloupe; U.S. Nat. Mus.). *New synonymy*

The four female syntypes of *Stephanoderes heveae* Hagedorn and the female holotype of *Cryptocarenus caraibicus* Eggers were compared to my material. All of these specimens represent the same species.

Schedl (1975, Ent. Blätt. 71:43) treated *C. lepidus* Wood as a synonym of *C. caraibicus*. These species are easily confused but quite distinct.

Hypothenemus setosus (Eichhoff)

Hypoborus (?) *setosus* Eichhoff, 1867, Berliner Ent. Zeitschr. 11:391 (Syntypes, Guadeloupe; one syntype in U.S. Nat. Mus., others lost with Hamburg Mus.)

Stephanoderes congonus Hagedorn, 1912, Rev. Zool. Afr. 1:337 (Lectotype, female; Eala, Congo; Tervuren Mus., present designation). *New synonymy*

Stephanoderes congonus Hagedorn was based on a syntypic series. Four of those syntypes are in the Musée Royal de l'Afrique Central, Tervuren, labeled as one "Holotypus" and three "Paratypus." These type designations, however, have not beeen mentioned in print and are considered invalid. The "Holotypus" is severely damaged but recognizable. All four specimens bear identical data labels: "Musée du Congo Belge; Eala; Rakusu (li?? 1140 M, 1911); D. Hevea brasiliensis." Because the first specimen is severely damaged, I designate the third specimen as the lectotype.

The above lectotype was compared to several of my series of *setosus* (Eichhoff) that previously had been compared directly to the only known syntype of *setosus*. Only one species is represented by this material. It is a species distinct from *javanus* (Eggers), as noted below. Other synonyms of *setosus* include *Stephanoderes obscurus* Eichhoff (nec Ferrari) and *S. depressus* Eichhoff.

Hypothenemus javanus Eggers,
new status

Stephanoderes javanus Eggers, 1908, Ent. Blätt. 4:215 (Lectotype. female; Java; U.S. Nat. Mus.. designated by Anderson and Anderson, 1971, Smithsonian Contrib. Zool. 94:16)

This species was placed in synonymy under *setosus* (Eichhoff) by Schedl (1962, Ent. Blätt. 58:204). Using the lectotype of *javanus* as a point of reference, I (Wood, 1972, Great Basin Nat. 32:51) added several additional synonyms. A reexamination of the types of *javanus, setosus*, and all synonyms, and 172 other specimens assigned to *setosus*, clearly indicates the existence of two easily distinguished species. *Hypothenemus javanus* (= *Stephanoderes obesus* Hopkins, *S. philippinensis* Hopkins, *S. bananensis* Eggers, *S. kalshoveni* Schedl, *S. subagnatus* Eggers) has a stouter body form (2.2 times as long as wide), only 12-18 coarse asperities on the anterior slope of the pronotum, 2-4 denticles on the anterior margin of the pronotum, and several minor differences in details of sculpture. It occurs in Indonesia, Philippines, Florida, Cuba, Jalisco (Mexico), Congo, Ghana, and the Camerouns. *Hypothenemus setosus* has the body 2.4 times as long as wide, more than 25 pronotal asperities, 6-8 denticles on the anterior margin of the pronotum, and other differences in details of surface sculpture. It occurs from Chiapas (Mexico) to Brazil, in the Congo, and in the Camerouns. Therefore, *javanus* must be restored as a valid name to designate the above species.

Microcorthylus minutus Schedl

Microcorthylus minutus Schedl, 1950, Dusenia 1: 160 (Syntypes, females; Nova Teutonia, Santa Catarina, Brazil; Schedl and Plaumann colls.)

Microcorthylus minutissimus Schedl, 1952, Dusenia 3:361 (Syntypes; Jamaica; Schedl Coll.). *New synonymy*

Female syntypes of *minutus* Schedl and *minutissimus* Schedl were compared directly to one another and to 36 other specimens from Veracruz, Honduras, Costa Rica, Panama, and Brazil. Only one small, distinctive species is represented by this material.

Pseudopityophthorus limbatus Eggers

Pseudopityophthorus limbatus Eggers, 1930, Ent. Blätt. 26:169 (Holotype, female; "R. d. M.," Mexico; deposited in Eggers collection, evidently now on loan to Schedl)

Pseudopityophthorus micans Wood, 1967, Great Basin Nat. 27:44 (Holotype, male; 96 km W. Durango, Durango, Mexico; Wood Coll.). *New synonymy*

The female holotype of *Pseudopityophthorus limbatus* Eggers and the female allotype of *P. micans* Wood were compared directly to one another and to 85 other specimens of this species and were found to represent only one species.

Xyleborus obliquus (LeConte)

Pityophthorus obliquus LeConte, 1878, *in* Schwarz. Proc. Amer. Philos. Soc. 17:432 (Holotype, female; Enterprise, Florida; Mus. Comp. Zool.)

Xyleborus gilvipes Blandford, 1898, Biol. Centr. Amer., Coleopt. 4(6):205 (Holotype, female; Zapote, Guatemala; British Mus.). *New synonymy*

Xyleborus brasiliensis Eggers, 1928, Arch. Inst. Biol., São Paulo 1:96 (Lectotype, female; Blumenau, Santa Catarina, Brazil; U.S. Nat. Mus.). *New synonymy*

Xyleborus illepidus Schedl, 1941, Rev. Zool. Bot. Afr. 34:402 (Holotype, female; Deutsch Ostafrika; Schedl Coll.). *New synonymy*

This species has been reported from areas disturbed by human activities in a pattern that suggests introduction. Its origin has not been established except that allied species are Neotropical. Its occurrence in Africa appears to be recent.

In establishing the above synonymy, the holotypes of *obliquus* (LeConte), *gilvipes* Blandford, and *illepidus* Schedl, the lectotype of *brasiliensis* Eggers, and 78 U.S., 46 Neotropical (Mexico, Guatemala, Colombia, Brazil), and 14 African (Congo) specimens were examined and compared directly. There is a certain amount of variability within this material, but the variation between series is no greater than it is within a series.

In addition to the above, the synonymy of this species with *linderae* (Hopkins) and *mexicanus* Eggers has already been established.

TAXA NEW TO SCIENCE

Dacnophthorus, n. gen.

This genus is distinguished from *Pityophthorus* Eichhoff by the very slender body form, by the very large, coarsely faceted eyes, by the large antennal club, with two partly septate sutures, by the pronotal summit being anterior to the middle of the pronotum and lacking a transverse impression posterior to it, by the distinctive elytral declivity, and by the very different habits.

Frons dimorphic, male convex above, impressed below, female uniformly shallowly concave to lower third, then weakly convex, upper area variously sculptured and ornamented by hair; eye very large, coarsely faceted, emarginate. Antennal scape slender, elongate; funicle 5-segmented, some specimens apparently 4-segmented; club large, much longer than scape, sutures 1 and 2 partly septate, 3 clearly indicated by setae and rather remote from apex. Pronotum elongate, summit anterior to middle, without a transverse impression behind summit. Scutellum rather large, flat. Elytra striate; declivity rather short, steep. Legs as in *Pityophthorus*.

TYPE-SPECIES.— *Gnathophthorus clematus* Wood.

NOTE.— The five species previously placed by me in *Gnathophthorus* must be transferred to this genus.

Araptus consobrinus, n. sp.

This species is distinguished from *attenuatus* Wood by the evenly convex elytral declivity (*attenuatus* has striae 1 impressed and interstriae 1 weakly elevated) and, on the female frons, by the coarser, more abundant, longer, yellowish vestiture.

MALE.— Length 1.4 mm (paratypes 1.4-1.7 mm), 2.7 times as long as wide; color very dark brown.

Frons similar to *attenuatus* except more nearly convex, punctures not as coarse, no indications of aciculation, median callus at upper level of eyes smaller, less strongly elevated.

Pronotum as in *attenuatus* except anterior margin armed by about eight serrations.

Elytra as in *attenuatus* except surface less brightly shining, strial punctures slightly larger. Declivity more evenly convex, punctures much smaller; striae 1 not impressed, interstriae 1 not elevated.

FEMALE.— Similar to male except frons much as in female *attenuatus* except frontal hair much more abundant, coarser, slightly longer, yellowish in color.

TYPE LOCALITY.— Six km or 4 miles N Tepic, Nayarit, Mexico.

TYPE MATERIAL.— The male holotype, female allotype, and 20 paratypes were taken at the type locality on 13-VII-1965, 1000 m, No. 241, from a shrub; seven paratypes are from 33 km or 21 miles N Juchitlan, Jalisco, Mexico, 3-VII-1965, 1300 m, No. 177, *Ficus* twigs 3 cm in diameter, all by me.

The holotype, allotype, and paratypes are in my collection.

Araptus micaceus, n. sp.

This species is distinguished from *obsoletus* (Blandford) by the strongly impressed frons, with a pair of epistomal calluses at the anterior articulations of the mandibles, by the smooth surface between punctures on the area above the eyes, and by the coarser strial punctures on the declivity.

MALE.— Length 1.4 mm (paratypes 1.3-1.4 mm), 2.6 times as long as wide; color light brown.

Frons as in *obsoletus* except much more strongly impressed, punctures in impressed area smaller, surface on area above eyes reticulate; epistomal calluses at anterior articulation of mandibles much larger.

Pronotum as in *obsoletus* except serrations on anterior margin much smaller (margin subcostate) and reticulation on posterior areas more strongly impressed.

Elytra as in *obsoletus* except strial punctures much larger, interstriae one and one-half times as wide as striae on disc, about twice as wide on declivity; impressed points obsolete on declivity.

FEMALE.— Similar to male except frons planoconvex on median two-thirds from level of antennal insertion to slightly above eyes, finely, closely punctured except impunctate on median line to upper level of eyes, punctured area bearing fine, rather long, moderately abundant hair; hair shorter, less abundant and covering a smaller area than in female *obsoletus*.

TYPE LOCALITY.— Los Corchos, Nayarit, Mexico.

TYPE MATERIAL.— The male holotype, female allotype, and seven paratypes were taken at the type locality on 10-VII-1965, 7 m elevation, No. 222, from a recently cut vine, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus costatus, n. sp.

This abberant species has a variable number of segments in the antennal funicle; it is also distinguished by the long, costiform pronotal asperities, by the stout body form, by the frons, and by other characters.

FEMALE.— Length 1.1 mm (paratypes, 1.1-1.2 mm), 2.3 times as long as wide; color dark reddish brown.

Frons rather strongly convex, an abrupt, moderately deep impression immediately above epistomal margin, epistomal margin distinctly elevated except for small median notch; surface smooth shining, sparsely punctured, punctures rather coarse, area above eyes somewhat reticulate; vestiture very sparse, short. Antennal funicle variable, 3-5-segmented; club ovate, small, sutures almost straight, 1 and 2 septate only at margins.

Pronotum 1.0 times as long as wide; widest at base, weakly arcuate on basal third rather strongly converging toward narrowly rounded anterior margin; anterior margin continuously costate; summit just behind middle, rather indefinite; asperities long, subcostate, confused, continued to basal fourth in median area; posterior areas strongly reticulate, punctures small, not close. Glabrous.

Elytra 1.5 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, punctures small, deep, spaced by one to two diameters of a puncture; interstriae smooth, shining, two to three times as wide as striae, punctures minute, confused, rather close. Declivity steep, convex; striae not impressed, punctures greatly reduced to obsolete; interstriae as on disc except punctures reduced to obsolete. Vestiture confined to declivity, of sparse, short, stout interstrial setae.

MALE.— Similar to female except epistomal impression usually more strongly impressed in lateral areas, with a weak median elevation dividing this impression.

TYPE LOCALITY.— Tapanti, Cartago, Costa Rica.

TYPE MATERIAL.— The female holotype, male allotype, and 12 paratypes were taken at the type locality on 2-VII-1963, 1300 m, No. 11a, from a liana, by me. Two paratypes are from 13 km SE Cartago, Cartago, Costa Rica, 3-VII-1963, 1800, from the same species of liana, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus inceptis, n. sp.

This species is distinguished by the simple male frons and declivity, by the female frontal vestiture and by the coarse pronotal and elytral punctures. It is not closely allied to other known species.

FEMALE.— Length 1.5 mm (male paratypes 1.5-1.6 mm), 2.7 times as long as wide; color very dark brown.

Frons basically convex except flattened on median half from epistoma to slightly above eyes; surface shining, punctures rather coarse, moderately close; vestiture rather sparse and short except on margins of upper half of flattened area forming a dense fringe of long yellow hair, longest setae equal in length to three-fourths distance from their bases to epistomal margin. Antennal club broadly obovate, 1.2 times as long as wide, suture 1 almost straight, 2 moderately procurved.

Pronotum 1.07 times as long as wide; widest on basal third, moderately arcuate from base to rather broadly rounded anterior margin; anterior margin armed by about six to eight low, basally contiguous teeth; summit at middle; asperities rather coarse, confused; posterior areas subrugose-reticulate, punctures coarse, deep, mostly spaced by distances equal to one-half diameter of a puncture, median line impunctate. Vestiture of sparse semirecumbent short hair in lateral and asperate areas.

Elytra 1.7 times as long as wide, 1.7 times as long as pronotum; sides almost straight and parallel on basal three-fourths, somewhat narrowly rounded behind; striae not impressed, punctures rather coarse, deep, occasional punctures not in row, spaced by less than diameter of a puncture; interstriae almost smooth, shining, impunctate except for an occasional puncture near declivity. Declivity steep, convex; striae not impressed, punctures reduced, about one-third as large as on disc, distinctly impressed; interstriae as on disc except 1 and 3 each with a row of fine punctures. Vestiture confined to sides and declivity, that on sides of minute strial hair, that on declivity of fine, rather short interstrial setae on odd-numbered interstriae.

MALE.— Similar to female except frons more uniformly convex, without brush of long hair; serrations on anterior margin of pronotum slightly larger.

TYPE LOCALITY.— Six km or four miles W Quiroga, Michoacan, Mexico.

TYPE MATERIAL.— The female holotype, male allotype, and one male paratype were taken at the type locality on 17-VI-1965, 2200 m, No. 72, from a shrubby herbaceous plant, by me.

The holotype, allotype, and paratype are in my collection.

Pityophthorus timidulus, n. sp.

This species is distinguished from *mendosus* Wood by the larger size, by the coarser pronotal punctures, and by slight differences on the elytral declivity. Both species are allied to *mandibularis* Schedl.

MALE.— Length 2.0 mm (paratypes 1.8-2.0 mm), 2.5 times as long as wide; color very dark brown.

Frons convex above eyes, upper half of area below upper level of eyes rather abruptly, strongly, transversely impressed almost from eye to eye, a smaller transverse impression in lateral areas immediately above epistoma; surface shining, coarsely, rather closely punctured; vestiture sparse except on epistoma. Antennal club oval, 1.3 times as long as wide, sutures 1 and 2 moderately arcuate, 2 at middle of club.

Pronotum 1.1 times as long as wide; sides on basal half almost straight, subparallel, rather broadly rounded in front; anterior margin armed by about 12 low serrations; summit at middle; asperities on anterior slope rather coarse, close, confused; posterior areas smooth, shining, with moderately abundant minute impressed points, punctures rather coarse, deep, moderately close, irregularly spaced by about one to two diameters of a puncture. Glabrous except a few setae on margins.

Elytra 1.6 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae 1 weakly, others not impressed, punctures rather small, deep, spaced by diameter of one puncture; interstriae smooth, shining, a few small punctures on 1 near declivity, others impunctate. Declivity steep, convex, shallowly bisulcate; interstriae 1 distinctly elevated, armed by a row of about seven rounded tubercles, 2 moderately impressed, slightly wider than 1, smooth, shining, devoid of punctures, 3 convex, as high as 1, armed as on 1, lateral areas with punctures somewhat confused. Vestiture confined to declivity, consisting of rather short, moderately coarse, sparse, interstrial setae on odd-numbered interstriae.

FEMALE.— Similar to male except frons below upper level of eyes shallowly, broadly, transversely impressed, surface regular, not granulate, punctures moderately fine, vestiture sparse, declivital sulcus much less strongly impressed, granules on interstriae 1 and 3 minute.

TYPE LOCALITY.— Volcan Chiriqui, Chiriqui, Panama.

TYPE MATERIAL.— The male holotype, female allotype, and 12 paratypes were taken at the type locality on 11-I-1964, 1800 m, No. 407, from a sapling 4 cm in diameter, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus mendosus, n. sp.

This species is distinguished from *timidulus* Wood by the smaller size, by the smaller pronotal punctures, by the shorter, stouter elytral bristles, and by the complete absence of tubercles on female declivital interstriae 1 and 3.

MALE.— Length 1.7 mm (paratypes 1.5-1.7 mm), 2.8 times as long as wide; color very dark brown.

Frons as in *timidulus* except callus at level of antennal insertion usually more strongly developed and with a small cusp at dorsomedian extremity. Pronotal punctures averaging slightly smaller than in *timidulus*. Elytra as in *timidulus* except declivital setae slightly shorter and distinctly stouter.

FEMALE.— As in female *timidulus* except frons less distinctly impressed, declivital granules absent, and declivital setae shorter and stouter.

TYPE LOCALITY.— San Isidro del General, San José, Costa Rica.

TYPE MATERIAL.— The male holotype, female allotype, and 18 paratypes were taken at the type locality on 5-XII-63, 1000 m, No. 282, from "Fósforo" leaf petioles, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus degener, n. sp.

This species is distinguished from the allied *timidulus* Wood and *mendosus* Wood by the much more weakly impressed male frons, by the strongly impressed elytral declivity, and by the finer pronotal punctures.

MALE.— Length 2.0 mm (paratypes 1.7-2.0 mm), 2.8 times as long as wide; color very dark brown.

Frons convex, but with abrupt, irregular, shallow, transverse impressions just below upper level of eyes and just above epistoma; surface subshining, coarsely, closely punctured; almost glabrous except at epistomal margin. Pronotum and elytral disc as in *timidulus* and *mendosus* except pronotal punctures much smaller, slightly closer; elytral declivity strongly bisulcate, interstriae 1 almost as high as wide, 3 higher than 1, each armed by a row of moderately coarse tubercles. Elytral vestiture as in *timidulus*.

Female.— Similar to male except median half of frons flattened below upper level, surface smooth, with punctures rather fine, close, deep, with rather abundant, fine, moderately long hair; declivital sulcus half as deep, interstriae 1 and 3 unarmed.

Type Locality.— Volcan Chiriqui, Chiriqui, Panama.

Type Material.— The male holotype, female allotype, and seven paratypes were taken at the type locality on 11-I-1964, 1800 m, No. 384, from a tree limb 8 cm in diameter, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus amiculus, n. sp.

This species is distinguished from *degener* Wood by the absence of sexual dimorphism, and by the different frons, pronotum, and other characters.

Male.—Length 1.8 mm (paratypes 1.7-1.9 mm), 2.7 times as long as wide; color reddish brown.

Frons convex above eyes, with median line smooth, impunctate, a median callus at upper level of eyes, area below upper level of eyes broadly, shallowly, transversely impressed to epistoma; surface almost smooth, punctures moderately coarse, close, deep; almost glabrous except along epistoma.

Pronotum 1.2 times as long as wide; outline as in *degener;* asperate area continued slightly into lateral portion of posterior half as weak rugae; posterior areas smooth, shining, with rather numerous impressed points, punctures rather fine, moderately close, median line impunctate. Sparse setae confined to asperate area.

Elytra 1.5 times as long as wide, 1.3 times as long as pronotum; outline as in *timidulus* Wood; striae not impressed, punctures rather small, deep, close, rows occasionally slightly confused; interstriae smooth, shining, slightly irregular, with a few impressed lines, impressed points moderately abundant, 1 with obscure subgranulate punctures almost to base, others with an occasional similar puncture. Declivity steep, strongly bisulcate, sulcus commencing slightly behind middle of elytral length; striae 1 and 2 with punctures reduced in size but clearly impressed; interstriae 1 almost as high as wide, 3 higher than 1, each armed by a row of about eight subacute tubercles of moderate size, 2 wider than 1, its surface ascending laterally, unarmed. Vestiture consisting of interstrial bristles on declivity, continued to middle of disc on odd-numbered interstriae; longest bristles rather slender, equal in length to twice width of an interstriae.

Female.— Similar to male in all respects.

Type Locality.— Guapiles, Limon, Costa Rica.

Type Material.—The male holotype, female allotype, and 12 paratypes were taken at the type locality on 22-VIII-1966, 100 m, No. 121, from a liana, by me. Eighteen paratypes are from Coatzocoalcos, Veracruz, Mexico, 26-VI-1967, 30 m, No. 103, liana, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus dissolutus, n. sp.

This species is distinguished from *explicitus* Wood by the finer frontal punctures, by the finer granules on the pronotal disc, and by the shallower declivital sulcus that is armed by finer granules.

Male.—Length 1.5 mm (paratypes 1.4-1.6 mm), 2.7 times as long as wide; color dark brown.

Frons convex, a fine median tubercle on epistomal process; surface strongly reticulate, punctures rather fine, deep, spaced by diameter of a puncture or more; vestiture fine, sparse, inconspicuous.

Pronotum 1.1 times as long as wide; widest on basal half, sides feebly arcuate, subparallel, rather narrowly rounded in front; anterior margin armed by about eight moderately coarse serrations; summit at middle, indefinite; asperities rather fine, confused; posterior areas strongly reticulate, punctures rather fine, moderately close. Vestiture confined to marginal and asperate areas.

Elytra 1.6 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae 1 weakly, others not impressed, punctures fine, distinct, decreasing in size posteriorly; interstriae almost smooth, with some indistinctly impressed lines, about three times as wide as striae on basal fourth, six times as wide near declivity. Declivity rather steep, shallowly bisulcate; striae 1 deeply impressed, punctures small, indistinct, surface ascending gradually to lateral convexity, striae 2 obscure; interstriae 1 almost as high as wide, almost smooth, with a row of fine tubercles, 2 and lateral areas shining, rather densely covered by impressed points, 3 slightly higher than 1, similarly armed. Vestiture of minute strial hair, and, on posterior half, interstrial bristles on odd-numbered interstriae; bristles sparse, rather fine, short.

FEMALE.— Similar to male except epistomal tubercle evidently absent, and declivital impressed points reduced or absent.

TYPE LOCALITY.— Thirteen km SE Cartago, Cartago, Costa Rica.

TYPE MATERIAL.—The male holotype, female allotype, and 27 paratypes were taken on 24-IX-1963, 1800 m, No. 201, from a liana 1 cm in diameter. Two paratypes are from Tapanti, Cartago, Costa Rica, 24-X-63, 1300 m, No. 244, liana; and six paratypes are from Volcan Chiriqui, Chiriqui, Panama, 11-I-1964, No. 394, in a sapling; all were taken by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus explicitus, n. sp.

This species is distinguished from *dissolutus* Wood by the coarser frontal punctures, by the larger granules on the pronotal disc, and by the deeper declivital sulcus that is armed by coarser granules.

MALE.— Length 1.5 mm (paratypes 1.5-1.7 mm), 2.7 times as long as wide; color very dark brown.

Frons as in *dissolutus* except punctures distinctly larger, spaced by less than diameter of a puncture. Pronotum as in *dissolutus* except granule on lateral margins of discal punctures distinctly larger. Elytra as in *dissolutus* except declivital sulcus deeper, wider, interstriae 2 not ascending laterally on lower half.

FEMALE.— Female similar to male in all respects.

TYPE LOCALITY.— Nine km NE Teziutlan, Puebla, Mexico.

TYPE MATERIAL.— The male holotype, female allotype, and 14 paratypes were taken at the type locality on 2-VII-1967, 1600 m, No. 143, from a liana, by me.

The holotype, allotype, and paratypes are in my collection.

Xyleborus californicus, n. sp.

This species almost certainly was introduced into California from another area, possibly from South America or southeastern Asia. Among North American species it might be confused with *pubescens* Zimmermann, but it is distinguished by the smaller size, by the more abundant pubescence, and by the reticulate-granulate interiors of the strial punctures on the declivity.

FEMALE.—Length 2.0 mm (paratypes 2.0-2.2 mm), 2.9 times as long as wide; color yellowish brown.

Frons rather strongly convex; surface strongly reticulate, a few small granules from epistoma to upper level of eyes. Vestiture of fine, sparse hair.

Pronotum 1.2 times as long as wide; sides almost straight and parallel on basal two-thirds, rather broadly rounded in front; anterior margin unarmed; summit in front of middle; anterior slope steep, rather coarsely asperate; posterior areas strongly reticulate, punctures small, shallow, rather close. Vestiture of fine, short, rather abundant hair.

Elytra 1.7 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on basal two-thirds, broadly rounded behind; disc occupying basal three-fourths; striae not impressed, punctures small, shallow, distinct, in rows, spaced by diameter of a puncture; interstriae three to four times as wide as striae, almost smooth, shining, punctures fine, in definite rows in some specimens, distinctly confused on basal half in others. Declivity steep, convex, general contours as in *pubescens;* strial punctures large, shallow, distinct, their interior surfaces reticulate-granulate; interstriae only slightly wider than striae, their punctures mostly replaced by minute granules on all interstriae, a few larger granules on 1, 3, and lateral areas; posterolateral margin rounded, with an indefinite row of scattered granules. Vestiture of rather abundant, short, fine hair, distinctly longer on margins of declivity.

Type Locality.— Stanford University, Palo Alto, California.

Type Material.—The female holotype and five female paratypes were taken at the type locality on 15-25-III-1944, by C. D. Duncan. One paratype is from Knight's Landing, Yolo Co., California, 10-I-1949, at light, by J. R. Fowler.

The holotype is in the California Academy of Sciences; three paratypes are in the Canadian National Collection, two are in my collection, and one is in the U.S. National Museum.

Specimens of this species were sent to Bright, Browne, and Schedl in an effort to associate it with a named species from another area, but without success. All agree that its anatomical characters, its current distribution, and the limited period it has been known in California strongly suggest that it was introduced from another area.

Xyleborus incultus, n. sp.

This species is distinguished from *pristis* Wood by the larger size, by the more distinctly impressed strial punctures, and by the declivital sculpture as described below.

Female.— Length 2.3 mm, 2.6 times as long as wide; color dark brown.

Frons and pronotum essentially as in *micarius* Wood except anterior margin of pronotum weakly produced at median line and armed by two larger serrations, punctures on posterior areas larger, at least twice as large as in *micarius*.

Elytra 1.5 times as long as wide, 1.3 times as long as pronotum; sides almost straight and parallel on basal 60 percent, narrowly rounded behind, a slight emargination at suture; striae not impressed, punctures small, distinctly impressed, spaced within a row by one to two diameters of a puncture; interstriae almost smooth, punctures fine, less than half as large as those of striae, moderately confused on basal third of disc, uniseriate behind. Declivity rather steep, convex; surface minutely granular on lower two-thirds, dull; interstriae 1 moderately elevated to near apex, armed by 15 or more small, pointed, confused denticles, 2 rather strongly impressed, armed on upper third by 4-6 similar, uniseriate denticles, 3 slightly elevated, armed as in 1 except denticles almost uniseriate, 4-9 each with a row of fine denticles, 3 and 9 join and continue submarginally to apex as a moderately strong elevation, its crest armed by a row of about four denticles. Vestiture largely confined to sides and declivity; of fine, short strial and slightly longer interstrial hair, longest setae about equal in length to width of an interstriae.

Type Locality.— Fort Clayton, Canal Zone, Panama.

Type Material.— The female holotype was taken at the type locality on 22-XII-1963, from a *Cecropia* branch, by me.

The holotype is in my collection.

Xyleborus molestulus, n. sp.

This species is distinguished from *crinitulus* Wood by the interstrial granules on the disc, by the uniseriate rows of elytral setae, and by other characters.

Female.— Length 2.0 mm (paratypes 2.0-2.2 mm), 2.2 times as long as wide; color dark brown.

Frons as in *crinitulus* except less strongly reticulate, more sparsely punctured. Pronotum about as in *crinitulus* except anterior margin armed by eight serrations, posterior areas very finely, shallowly punctured.

Elytra 1.2 times as long as wide, 1.3 times as long as pronotum; sides almost straight and parallel on basal two-thirds, broadly rounded behind; striae not impressed, punctures rather small, shallow, distinct, spaced by one to two diameters of a puncture; interstriae almost smooth, three times as wide as striae, each with a uniseriate row of fine tubercles from base to apex. Declivity occupying posterior half of elytral length, moderately steep, broadly convex; sculpture as on disc except striae 1 feebly impressed; posterolateral margin acutely, subcrenulately elevated from apex to interstriae 7. Vestiture of interstrial rows of long, erect hair from base to apex, alternate setae in each row twice as long as distance between rows and alternating with setae half that length on both disc and declivity.

Type Locality.— Barro Colorado Island, Canal Zone, Panama.

Type Material.— The holotype and six paratypes were taken at the type locality on 27-XII-1963, No. 348, from a tree branch. Four paratypes are from Fort Clayton, Canal Zone, Panama, 22-XII-1963, No. 363, from a tree branch; three paratypes are from Madden Forest, Canal Zone, Panama, 2-I-1964, 70 m, No. 365, from a tree seedling; and one paratype is from 13 km (8 miles) S El Hato del Volcan, Chiriqui, Panama, 7-I-64, tree seedling. All were taken by me.

The holotype and paratypes are in my collection.

Xyleborus tristiculus, n. sp.

This species is distinguished from *molestulus* Wood by the more slender body, by the larger pronotal punctures, and by the differences on the elytra described below.

Female.— Length 2.0 mm (paratypes 1.9-2.1 mm), 2.4 times as long as wide; color brown.

Frons about as in *molestulus* except uniformly, more strongly reticulate.

Pronotum 1.02 times as long as wide; as in *molestulus* except median part of anterior margin weakly produced, four median serrations distinctly larger, and punctures on posterior areas distinctly larger, spaced by at least two to six diameters of a puncture; vestiture finer, longer, more abundant.

Elytra 1.3 times as long as wide, 1.3 times as long as pronotum; similar to *molestulus* in outline except more narrowly rounded behind; about as in *molestulus* except discal interstriae not as smooth, interstrial punctures very feebly if at all granulate, declivital striae slightly smaller, interstriae not as smooth, interstrial tubercles more closely spaced, averaging smaller. Vestiture consisting of rather long, fine, semirecumbent strial hair on disc and declivity, and rows of erect interstrial setae on declivity and posterior half of disc, each seta coarser and distinctly longer than those of striae, distance between rows and between setae within a row about two-thirds length of a seta.

Type Locality.— Brazil, 12° 49′ S 51° 46′ W (not 12° 31′ S as given on label).

Type Material.— The female holotype and four female paratypes were taken at the type locality 8-XI-1968, No. C-47, 22-XI-1968, No. D-35, 24-IX-1968, Nos. 170, 172, 2-XII-1968, No. E-18, all by R. A. Beaver.

The holotype is in the British Museum (Natural History), one paratype is in Museo de Zoologia, Universidade de São Paulo, and three paratypes are in my collection.

CORRELATES OF BURROW LOCATION IN BEECHEY GROUND SQUIRRELS

Donald H. Owings[1] and Mark Borchert[1]

Abstract.— Partial correlation analysis indicates that Beechey ground squirrels show a strong preference for digging burrows under and around large objects, may show a weaker tendency to locate their burrows under the cover of tree canopies, and avoid digging burrows in areas with both tree-canopy and ground cover (stones, logs). These relationships hold for large but not small burrow systems. The need for unobstructed visual surveillance and an autumn food supply are proposed to be determinants of these preferences.

Beechey ground squirrels (*Spermophilus beecheyi*) appear to show preferences for areas with certain characteristics for the location of their burrows. At least three factors have been suggested to affect the choice of burrow sites: (1) burrows are often constructed under large objects such as stones or logs (Linsdale 1946: 9); (2) good drainage is said to be important, which is best provided by sloping terrain (Tomich 1962); (3) burrows often seem to be concentrated under the cover of tree canopies (Fitch 1948). One purpose of the research reported here was to quantitatively assess the relationship between burrow location and these three independent variables—ground cover (stones, logs), slope of terrain, and tree canopy cover. In addition, we felt that the effect of ground and tree cover might interact, or at least be additive, in areas in which these factors physically overlapped. We therefore added a fourth independent variable (common cover) to the analysis which consisted of a measure of the amount of area having ground and tree cover in common.

It is probably true, though, that burrow systems of different sizes may differ in their relationship with these variables. Small systems, for instance, may be established by young squirrels who have moved into less than optimal habitat during dispersal, or by adults for refuge from predators when feeding in the open (Fitch 1948; Carl 1971). A second purpose of this research was to divide the burrow systems into size categories for separate analysis.

Study Area

This study was done in the Department of Zoology Experimental Wildlife Area on the campus of the University of California at Davis (elevation about 15.85 m; 38° 32′: N, 121° 47′: W). The study plot was located in the 82-m wide original bed of Putah Creek which is now permanently dry. This area contained numerous trees (principally black walnut, *Juglans hindsi*, and valley oak, *Quercus lobata*), grasses (principally ripgut brome, *Bromus rigidus*, with some Italian ryegrass, *Lolium multiflorum*, and wild oats, *Avena fatua*), and thistle (*Centaurea solstitialis* and *Silybum marianum*), as well as logs, and included most of both sloping sides of this cross-section of the bed. A substantial population of squirrels inhabited this area: 44 were trapped and marked in 0.60 ha in the spring of 1973. This area was being mapped in preparation for behavioral studies.

Methods

Our procedure was to lay out a grid of 9.14 x 9.14 m squares and to map on graph paper the location of all burrow entrances, the location and size (to scale) of ground cover, and the outer limits of tree canopies for each of 50 of these squares. We derived measures of ground cover area, tree canopy area, common area, and number of burrow entrances from these maps. Slope was measured over uniform sections of the area; new measures were taken wherever significant changes in slope occurred.

We assumed that size of burrow system was positively correlated with numbers of entrances. We used a portable blower (Steco Model DS-5) and nontoxic smoke bombs (Superior 0.5 min) to assess the number of entrances in a system by blowing smoke into one entrance and designating as connected to that entrance all burrows emitting smoke.

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Results and Discussion

In order to minimize the problem of correlated independent variables, we calculated partial correlation coefficients. This statistic provides a measure of the correlation of burrows with each independent variable, while holding the effects of the remaining independent variables constant. The results of this analysis can be found in Table 1. The first (uppermost) row includes burrow systems of all sizes and suggests that Beechey ground squirrels (1) show a strong preference for digging burrows under and around large objects, (2) may show a weaker tendency to locate their burrows under the cover of tree canopies, but (3) avoid digging burrows in areas with both tree-canopy and ground cover.

In order to test the hypothesis that the larger systems were the ones most consistently associated with our independent variables, we successively separated increasing sizes of small systems and analyzed them separately from the larger systems. The results of these analyses are presented in the remaining rows of Table 1. It is clear that there is little effect upon the relationship between burrows and ground cover of deleting from the analysis burrow systems with 1 to 4 entrances. However, deletion of 5-entrance systems from the large-system analysis caused a large drop in the correlation coefficient. Addition of 5-entrance systems to the small-system analysis results in the first significant correlation with ground cover. We conclude that small burrow systems tend not to be associated with ground cover, whereas larger systems (5 or more entrances) do.

The negative correlation with common cover and the positive correlation with tree cover followed the same pattern when system size was manipulated. As a result, we conclude that it is principally the larger systems which tend not to be associated with areas having overlapping ground and tree cover, but which are located under or near tree cover.

Our behavioral observations indicate that squirrel concentration was correlated with burrow concentration, and G. L. Hunt (unpubl. data) has quantitatively documented this in another location ($r = 0.80 - 0.85$ between numbers of squirrels and burrow entrances). We assume then that our data indicate microhabitat selection by these ground squirrels.

We feel that the strongest determinant of this propensity to live in the vicinity of ground cover is the visibility it provides. Hunt (unpubl. data) has gathered considerable support for the hypothesis that Beechey ground squirrels in a much more open area tend to concentrate in locations in which their ground level view (probably of approaching predators) is least obstructed by locating themselves

TABLE 1 Partial correlation coefficients between the numbers of burrow entrances from burrow system of various sizes (dependent variable) and the independent variables (1) slope, (2) ground cover, (3) tree cover, and (4) common cover. Size of burrow system is expressed as the number of entrances to the system.

Burrow system sizes included in analysis	Number of entrances included in analysis	Partial correlation coefficients of entrances with			
		Slope	Ground cover	Tree cover	Common cover
1-39	261	-0.067	0.620*	0.231	-0.382*
1	23	0.010	0.012	0.325*	-0.220
2-39	238	-0.067	0.613*	0.187	-0.354*
1-2	39	0.106	-0.116	0.051	0.069
3-39	222	-0.089	0.636*	0.225	-0.398*
1-3	54	-0.009	-0.089	0.054	0.013
4-39	207	-0.064	0.629*	0.216	-0.383*
1-4	74	0.109	0.053	0.029	0.043
5-39	187	-0.100	0.591*	0.211	-0.378*
1-5	92	0.079	0.407*	0.134	-0.250*
6-39	169	-0.089	0.484*	0.164	-0.271*
1-6	107	0.025	0.369*	0.122	-0.238*
7-39	154	-0.071	0.486*	0.164	-0.266*
1-7	127	0.027	0.316*	0.246*	-0.233
8-39	134	-0.075	0.503*	0.104	-0.265*

*With $df = 48$ an r of ± 0.236 is significantly different from 0.0 at $p = 0.05$.

appropriately on slopes and in areas of low vegetation. Linsdale (1946: 63) has argued that the disappearance of squirrels from the Hastings Reservation at the termination of regular grazing was caused by the visual obstruction of the taller grass. In our area the grass regularly reaches heights of a meter, but the squirrels appear to compensate for this by using the numerous promontories (ground cover) for visual surveillance when disturbances occur, as well as when simply lying, sitting, or grooming. A similar factor could account for the avoidance of common cover, since a considerable amount of the ground cover beneath tree canopies was made up of small, highly branched logs, sticks, and twigs. Some of the ground cover was beneath canopies which almost reached or did reach ground level. Such cover is often neither readily mounted nor useful for visual surveillance since the canopy would often obstruct the view. The same factor might also explain our failure to find a relationship with slope. It is possible that the preferences of squirrels in flat land for embankments is related more to enhanced visibility than to drainage (Hunt, unpubl. data).

Visibility seems an unlikely determinant of the preference for tree-canopy cover. We concur with Fitch's (1948) suggestion that this preference is related to the food available in the trees, i.e., acorns in his case, and acorns and walnuts in ours. These are the primary food sources in the fall when the grass, grass seeds, and forbs eaten in the spring are no longer available (Schitoskey 1973).

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ARACHNIDS AS ECOLOGICAL INDICATORS

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Abstract.- In three ecological studies in the southern parts of Nevada, Idaho, and Utah, spiders of 138 species, scorpions of 10, solpugids of 29, and phalangids of 2 species were obtained by pitfall capture. Significant differences in species occurrence were noted between the three geographic and ecologically distinct areas. Within each geographic area, arachnids differed in species occurrence and abundance in different plant communities. Only three species of spiders and four species of scorpions were common to all three geographic areas.

This paper summarizes species distribution of arachnids captured in can pit traps in the major plant communities of three geographic areas—southern Nevada, southern Idaho, and southern Utah—during the periods of 1959 to 1966, 1966 and 1967, and 1971 to 1973, respectively. Details of the equipment and techniques used and specific results of the studies in each area are discussed in published articles listed in the references section of this paper. The comparative results of these three studies are summarized in Tables 1 to 4.

Summary Discussion

Only three spiders—*Calilena restricta*, *Euryopis scriptipes*, and *Haplodrassus eunis*—were common to all three areas. Fifteen other species were common to Nevada and Utah, seven to Nevada and Idaho, and six to Idaho and Utah. *Paruroctonus boreus* was the only scorpion found in all three study areas. Four other species were common to Nevada and Utah, one to Nevada and Idaho, and one to Idaho and Utah. None of the 29 species of solpugids was found in all three areas. Two species were common to Nevada and Utah, and two to Nevada and Idaho.

Apparently the habitat preferences of most species of these arachnids are so unique that even at similar latitudes and in similar vegetative types the environmental factors are sufficiently different to influence species occurrence. Such differences in geographic distribution may be expected more with groups such as scorpions and solpugids whose capability for migration is extremely limited, whereas spiders through their ballooning adaptations would be expected to be more widely distributed.

Within each geographic area, arachnids differ in species and abundance in relationship to the different plant communities. Where similar predatory niches are

Table 1. No. of collection attempts and specimens of arachnids collected in three geographic areas.

Area	Trap periods[1]	Spiders	Scorpions	Solpugids	Phalangids
Nevada	52,080	5,600	1,471	1,000	575
Idaho	20,490	500	282	72	0
Utah	3,590	829	198	34	0

[1]No. pit traps x no. 24-hr periods operated.

Table 2. Species diversity of arachnids in three geographic areas.

Area	No. species collected			
	Spiders	Scorpions	Solpugids	Phalangids
Total species collected	138	10	29	2
Nevada	94	9	28	2
Idaho	42	1	6	0
Utah	40	5	3	0
In both Nevada & Utah	15	4	2	0
In both Nevada & Idaho	7	1	2	0
In both Idaho & Utah	6	1	0	0
Common to all areas	3	1	0	0

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TABLE 4. Ecological predominance of arachnid species in three geographic areas.

	Most Widespread	Most Abundant
	Spiders	
Nevada	*Calilena restricta*	*Psilochorus utahensis*
Idaho	*Calilena restricta*	*Schizocosa avida*
Utah	*Psilochorus utahensis*	*Psilochorus utahensis*
	Scorpions	
Nevada	*Vaejovis confusus*	*Vaejovis confusus*
Utah	*Paruroctonus boreus*	*Paruroctonus boreus*
	Solpugids	
Nevada	*Hemerotrecha californica*	*Hemerotrecha californica*
Idaho	*Eremobates septentrionis*	*Eremobates septentrionis*

TABLE 3. Arachnid abundance in predominant plant communities.

	Most Species	Fewest Species
	Spiders	
Nevada	Blackbrush	Juniper
Idaho	Sagebrush	Rabbitbrush
Utah	Juniper	Blackbrush
	Scorpions	
Nevada	Mixed	Juniper
Utah	Blackbrush	Sagebrush
	Solpugids	
Nevada	Hopsage	Blackbrush
Idaho	Rabbitbrush	Goosefoot

demonstrated, as between spiders, scorpions and solpugids, the occurrence of each group would be expected to differ within the same community. For example, in Nevada the spiders were most common in the blackbrush and mixed communities, whereas the solpugids were least common in the blackbrush and most common in the pinyon-juniper and hopsage-wolfberry where the spiders and scorpions were not abundant. In Idaho the spiders were most abundant in the sagebrush and least in the rabbitbrush, whereas the solpugids were most abundant in the rabbitbrush. In Utah the scorpions were most abundant in the blackbrush, whereas the spiders were least abundant there.

The relationship of arachnid species to vegetative type is not a direct one, but an interrelationship between a variety of environmental-influencing factors such as cover, food, moisture, temperature, and edaphic conditions. Specific data on these influencing factors are not available for correlation with the results summarized here. Such data are necessary for complete ecological interpretations, and such correlative studies are desirable for a better understanding of these interrelationships. However, knowledge of species diversity alone in different geographic areas as well as predominant plant communities is sufficient to determine ecological indicators that may be monitored relative to changes in environmental quality.

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NOTES ON THE GENUS *BOMBYLIUS* LINNAEUS IN UTAH, WITH KEY AND DESCRIPTIONS OF NEW SPECIES (DIPTERA: BOMBYLIIDAE)

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ABSTRACT.— A key to the Utah species of *Bombylius* is presented. *Bombylius heximaculatus, nigriventris, montanus, abdominalis, aestivus,* and *auriferoides,* new species, and *lancifer kanabensis,* subspecies new, are described from Utah. *Bombylius lassenensis,* new name, is proposed to replace the preoccupied *B. pallescens* Johnson and Maughan.

The first comprehensive paper on Utah *Bombyliidae* (Maughan 1935) lists six species in the genus *Bombylius* Linnaeus, with the identity of a seventh left in doubt because of the small amount and poor condition of the material available for study. Additional collecting of specimens in good condition showed this species might be *B. clio* Williston, but the specimens are not well enough preserved to include in our present key. The alternate species, *B. fascialis* Cresson, has been collected in abundance by us. These results were published in a subsequent paper (Maughan and Johnson 1936). Still further collecting has added much to our knowledge of this genus as it occurs in the northern Great Basin area of Utah, but its status in the southern Great Basin and in the Colorado River drainage system is still little known. We feel, nevertheless, that publication of our available information at this time is worthwhile as it may stimulate future collectors to study this group of flies. In this paper we discuss briefly the forms previously known to occur in the state, describe seven new taxa, and present a key for their identification. In addition, we use this opportunity to give a new name to the homonym *Bombylius pallescens* Johnson and Maughan.

A large part of the work on this paper was completed eight to ten years ago. Unfortunately, changing circumstances and the illness and death of Elmer Johnson slowed progress on its completion. We had completed the key and most of the descriptions prior to that time. In May 1975 I (Lucile) assumed the responsibility, in cooperation with Dr. Vasco M. Tanner of Brigham Young University (BYU), of completing this paper so it could be published. I have completed the remaining species descriptions and revised the paper where it seemed advisable.

The holotypes, allotypes, and paratypes dealt with in this paper are in the Brigham Young University entomological type collection.

The extensive collection of bee flies which we built up over the past 40 years has been transferred to Brigham Young University where it has been carefully curated by Dr. Tanner and his associates and is available for study. Many of the genera represented in the collection include apparently undescribed species which will hopefully be the subject for further research. Much of our collection over the years and all of the types we have named in other genera were previously deposited in the Brigham Young University Life Sciences Museum.

Nearly all of the material dealt with in this paper is from Utah, with a few specimens from neighboring states, largely collected by Mr. Johnson, some by both of us, and a few by other collectors.

Sincere thanks are expressed to those who have aided and given encouragement toward the completion of this paper: to our family; especially to Dr. Tanner for his advice and active assistance in caring for our collection; and to Mrs. Reginald H. Painter, who has been a source of strength and inspiration.

Key to the Species of *Bombylius* Discussed in this Paper

1. Wings with the anterior half brown or blackish, this colored area with a sinuous and sharply defined posterior margin .... *major* Linneaus

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Wings with brown area not sharply defined, nearly hyaline, or spotted 2

2(1). Wings with five to seven distinct dark spots on veins and crossveins in hyaline portion 3

Wings at most faintly spotted on veins and crossveins other than the r-m crossvein and free part of vein Cu_1 4

3(2). Wings with dark spot near distal end of vein R_{2-3}; heavily tomentose, female with golden tomentum on front; usually in the mountains or foothills .... *albicapillus albicapillus* Loew

Vein R_{2-3} without dark spot near its end; sparsely tomentose, female with pale yellowish tomentum on front; usually found in the foothills and valley floors .... *heximaculatus* n. sp.

4(2). Face prominent, facial pile wholly black 5

Face pollinose, facial pile at least in part pale 11

5(4). Pile of dorsum mostly pale yellow to golden; legs except bases of femora and spots on knees yellow; female with large trapezoidal area on front shining; both sexes with median line of pale tomentum on abdominal dorsum; halteres pale brown to yellow .... *fascialis* Cresson

Pile of dorsum not as above; usually with a more or less prominent line of brown or black hairs extending from base of wings forward onto occiput 6

6(5). Males 7

Females 9

7(6). Pile of venter black, that of dorsum pale gray; no tufts of black pile on sides of abdomen visible from above; relatively large species (9-12 mm); frequents the foothills .... *nigriventris* n. sp.

Pile of at least first three ventral abdominal segments pale; tufts of black pile on sides of abdomen visible from above 8

8(7). Pale pile of dorsum dark yellowish gray, always several on posterior callosities black; line of dark hair from wing onto occiput usually broad and prominent; prominent tufts of black pile on hind angles of second and third terga; band of black pile on front of two and often on three also; frequents mountains .... *lancifer lancifer* Osten Sacken

Pale pile of dorsum nearly white, on posterior callosities may be occasional black hairs; line of dark hairs from base of wing onto occiput thin and inconspicuous; tufts on sides of terga prominent on anterior angles of third segment only, on fourth visible from venter only .... *lancifer kanabensis* n. ssp.

9(6). Relatively large species (9-12 mm); lower frontal patch almost obsolete, the sparse scales mostly pale brown; patches of dense white or nearly white tomentum on second and following segments form a prominent median line on abdominal dorsum; tomentum of remainder of dorsum hairlike and relatively sparse; frequents foothills .... *nigriventris* n. sp.

Smaller species (7-10 mm); lower frontal patch prominent, of black hairlike scales; abdomen with crossbands of more or less dense pale scales on posterior half of second and following segments, median line of scales evident but not prominent 10

10(9). Pale hairs on dorsum mostly dark grayish yellow, many black hairs on mesonotal disc and posterior callosities; some of pale tomentum of abdominal dorsum noticeably pale brown; dorsum appears banded black and pale due to sparse dark tomentum in bands of black pile on anterior part of terga ..... *lancifer lancifer* Osten Sacken

Pale hairs of dorsum nearly white, few if any black hairs on mesonotal disc and posterior callosities; tomentum of posterior half of second and following abdominal segments whitish gray, that of anterior half of second and third segments tinged with tan, covering segments ..... *lancifer kanabensis*, n. ssp.

11(4). Lower frontal patch white to grayish 12

Lower frontal patch yellow to golden 14

12(11). Facial pile wholly white; base of wings brownish; pre- and postalar and scutellar bristles prominent, brown; female with many heavy bristles on upper mesopleura ..... *montanus* n. sp.

At least some black hairs below antennae and along facial orbits; base of wings blackish 13

13(12). Most of pile of face black, only that on oral margin yellowish; entire frontal triangle of male covered with dense appressed white scales; on the female these scales are found only between antennae and eyes; dark of wings fills anteroproximal one-third or more of wing; dark spots present on r-m crossvein and free part of vein Cu_1 ..... *metopium* Osten Sacken

Most of pile yellow to white, only a narrow band of hairs below antennae and on facial orbits black; middle of frontal triangle of male devoid of dense appressed tomentum; only anteroproximal fifth or less of wing dark, no brown clouds on veins or crossveins; prominent crossbands of black pile on abdominal dorsum ..... *abdominalis* n. sp.

14(11). At most bases of femora dark, rest of legs reddish tan 15

Legs black 16

15(14). Pile at base of wings golden; dark anterobasal part of wing with distinctly reddish brown cast; male genitalia red, slightly darker than femora; late summer species (August) ..... *aestivus* n. sp.

Pile at base of wings grayish yellow to white, male genitalia brown to black 17

16(14). Abundant erect pile of front, first two antennal segments and wide band below lower frontal patch black and very long in both sexes, female with mixed pale and black on front; pale gray species, female with nearly completely hyaline wings ..... *lassenensis* new name

No erect pile on front in male; pile of face, appressed hairlike tomentum on front of both sexes, and erect pile of female all same pale color; black pile on antennae and narrow band below lower frontal patch ..... *aurifer pendens* Cole

17(15). Halteres yellow; third antennal segment of female widest at or beyond middle, with sides nearly parallel for three-fourths of its length, then tapering abruptly to end; pile of front and ocellar tubercle of female wholly yellow; dark color in wing of male does not extend beyond tip of vein R_1 ..... *aurifer aurifer* Osten Sacken

Halteres various shades of brown; third antennal segment of female widest before the middle, not evenly tapering toward end; pile of front and ocellar tubercle of female mixed black and yellow; shining white scales form complete band above antennae between eyes; dark color in wing of male more or less fills all of cell R_1 ..... *auriferoides* n. sp.

Bombylius heximaculatus, n. sp.

Wings with five or six distinct black spots in the hyaline area or bordering the dark color. Legs mostly red. 9-12 mm in length.

Female.— Black. Head gray pollinose, occiput densely so; lower frontal patch black, very sparse; tomentum of front sparse, golden; pile of antennae, ocellar tubercle, front, and face black, a few pale hairs around the oral opening; pile of occiput white or nearly so, a patch of brown to black near lower hind angle of eye; segments 1 and 2 of antennae about same width, 2 one-third as long as 1; segment 3 somewhat wider, about one-fourth longer than first two combined, widest at about first third, sides of apical third about parallel; proboscis about five-sixths as long as head and body combined.

Mesonotal disc velvety black; pile long, dense on anterior one-third and sides; sparse, gray mixed with a little black on center and scutellum; with some sparse decumbent grayish yellow tomentum; pleura densely gray pollinose, lavender glints in some lights; a dense patch of mixed black, brown, and gray pile on upper mesopleura, just before wings, continuous with dark hairs of lower occiput; most of rest of pleura naked or nearly so, the sparse pile mostly pale, a few black hairs intermixed.

Wings with anteroproximal one-third smoky, remainder gray hyaline; dark spots on veins at r-m crossvein, base of R_4, at junction of $M_1 + R_5$, at free part of M_2, at cubital end of median crossvein, and at free part of Cu_1. Basicostal pile black, a few pale hairs on sides of costa. Halteres brown.

Legs dark red, hind femora yellowish except knees, others brownish red, darker basally, and tarsi dark; pile of fore coxae pale yellowish gray, of middle coxae mixed black and pale, and on hind ones only a few black in the gray; of rest of legs black; bristles black; tomentum pale, like the pile.

Abdomen faintly gray pollinose; pile dense on sides, lateral fringe mostly almost white on sides of first, anterior half of second, fifth, and following segments, considerable black pile mixed in on sides of posterior half of second and on third and fourth; pile of dorsum mostly short pale yellowish gray, with many long black hairs on hind margins of second and following segments. Most of pale pile of venter black, a few pale hairs on first segment; sparse tomentum pale yellow.

Type.— Female holotype: Alpine, Utah Co., Utah, 20 May 1955 (L. M. Johnson). Paratypes: 4 ♀ same data.

Several males were collected but became damaged so no description will be attempted at this time. The males are paler, with less black and pale pile on abdominal dorsum and more black pile on sides. Pile of venter is yellowish gray. Females are more tomentose. There is some variation in both sexes in the amount of dark pile at hind angles of eye and on mesopleura between the wing and head.

Bombylius nigriventris, n. sp.

Black. Anteroproximal third of wings blackish, gradually evanescent behind. Most of pile pale yellowish gray, that of abdominal venter mostly black. Length 6-12 mm exclusive of proboscis. Proboscis long, three-fourths as long as to fully as long as body and head.

Male.— Head black, face except upper and outer margin brown. Front and dark margin of face faintly grayish pollinose. Occiput and genae yellowish gray pollinose. Pile of face, front, antennae, a row along upper orbits on occiput and ocellar tubercle black. That of rest of head pale, faintly yellowish gray, a patch of brown hair on lower occiput. Lower frontal patch of short, black hairlike scales. Antennae cylindrical, segment 1 a little more than twice as long as broad, segment 2 same width, about as long as broad, segment 3 somewhat narrower, slightly more than twice as long as first two combined, widest at its proximal one-fourth, sides of distal two-thirds almost parallel; first segment long pilose, segment 2 very short fine pilose, segment 3 with a few short fine hairs on its upper side on distal half. Palpi black, black haired.

Pile long and dense on anterior third, relatively short and sparse on remainder of mesonotum, very pale yellowish gray, some dark hairs scattered among pale in center of mesonotal disc. Pile of pleura dense above, more sparse below, lower pteropleura bare, mostly nearly white, that on sterno- and hypopleura slightly yellowish. A band of mixed brown and pale hairs extending from the base of wing forward to join with patch of brown hairs on lower occiput. Pile of scutellum same color, occasional darker hairs along hind margin.

Dark of wings fills alula, basal third of axillary, two-thirds of anal cell, base of fourth posterior to base of discal past r-m crossvein to tip of subcostal cell. Remainder of wing gray hyaline, veins dark brown. Basicostal pile mostly black, longer and pale at base, a few pale hairlike scales beneath. Halteres brown.

Coxae and base of femora dark brown, remainder of legs reddish brown; bristles black; pile of coxae pale, many dark hairs intermixed on middle pair, that on femora mixed pale and dark brown; tomentum of legs pale yellowish gray, a line of brown scales on facies of femora.

Abdomen blue black; pile of dorsum long, dense, pale faintly yellowish gray, lateral fringe on second and third and a few hairs on hind margins of second and following segments black, somewhat more numerous on fifth and sixth terga. Pile of first two sternites pale, of rest of venter and on genitalia black, a very few pale yellowish hairlike scales intermixed.

Female.— Less pilose and more tomentose than male. Vertex, front, and dark upper and outer margin of face brown pollinose. Antennal segment 1 about two and one-half times as long as wide; segment 2 same width, as long as wide; segment 3 widest at proximal third, thence tapering evenly to short onion-shaped style. Tomentum of front yellow, a few brownish scales near orbit in lower frontal patch; that of occiput nearly white. Pile of head as in male, except that there are a few pale hairs on front along orbits.

Mesonotum and scutellum with moderately dense, pale grayish yellow curly appressed hairlike tomentum. The band of darker pile extending from base of wing to occiput is yellowish brown, intermixed with a few black hairs. Wings paler than in male, basicosta has more pale tomentum.

Pile of abdomen much coarser than in male, pale hairs mostly more yellow; many more black hairs, that of fifth and sixth terga mostly black; black hairs of lateral fringe of second and third terga confined to hind angles; lateral fringe of fourth and fifth segments white.

Dense median patches of faintly yellow to white tomentum on second and following terga form a prominent line down middle of abdominal dorsum. Pale hairlike tomentum on hind margins of first two and in median spots on following sternites; rest of sparse tomentum of venter black.

Types.— Male holotype: Alpine, Utah Co., Utah 23-V-1955 (D. E. Johnson), female allotype, topotypical, 20-V-1955 (D. E. Johnson), paratypes 13♂♀, topotypical, 11-V-1954, 16-V-1954, 18-V-1954, 22-V-1955, 19-VI-1955, (D. E. and L. M. Johnson); 2♂ 1♀ Dry Canyon, Salt Lake Co., Utah; 1♂ 1♀ Fort Douglas, Salt Lake Co., Utah, 10-V-1933, 6-V-1940 (W. Anderson); 2♂ Oak Creek Canyon, Millard Co., Utah, 24-V-1957 (D. E. Johnson); 1♂ Mt. Carmel Junction, Kane Co., Utah. 21-V-1957 (D. E. Johnson).

In addition to the variation in size, there is some variation in the amount of black pile on the mesonotal disc and hind margins of the abdominal terga in the males, and in the amount and color of tomentum on the abdominal dorsum of the females. In both sexes there is some variation in the amount and color of the dark pile which forms the conspicuous dark line from the base of the wings forward onto the lower occiput.

This species has the same type of face and wings as *lancifer*, but can readily be separated from that species by its larger size, by the absence in both sexes of the crossbands of black pile found on the hind margins of the second and third terga of *lancifer*, by the presence of mostly dark vestiture on the abdominal venter, where *lancifer* is mostly pale, and by the presence in the female of the prominent median line of white tomentum on the abdominal dorsum. Moreover, *lancifer* is a species of the mountains, while *nigriventris* appears to be confined to the foothills and valley edges, and is on the wing about a month earlier in the season.

While hovering, the females of this species produce a sound somewhat lower in pitch than the hum of a honeybee, and of a different quality, being more of a buzz than a hum. The hovering males produce a hum considerably higher than that of the bee. This high-pitched hum was audible to us for a distance of forty or fifty feet, and was frequently used as a means of locating specimens. Frequently males were found hovering or darting about some 7 to 12 or so feet above a given small area. We found our first female, as well as several subsequent ones, resting on the ground beneath such a hovering male. We did, indeed, use the males as guides to the females, collecting first the female and then the male. Another species of *Bombylius heximaculatus* n. sp., was present in the same habitat as *nigriventris*, and was found in far greater numbers. There was sufficient difference in the sounds produced by the two species to readily recognize and locate *nigriventris* specimens by the lower pitch.

The types were taken about one mile west of the village of Alpine, at an elevation of 5,340 feet. The site is a narrow unplowed strip alongside a road through agricultural lands. The whole area is foothills of the Wasatch Mountains above the highest level of Pleistocene Lake Bonneville. With the exception of Mt. Carmel Junction, the other collection sites are also foothill areas of the Wasatch, at elevations between 5,300 and 6,000 feet. The elevation at Mt. Carmel Junction is listed as 5,241 feet.

Although other species were available, the only flowers at which we saw these beeflies feeding were those of *Phlox longifolia*. Wherever we have found *nigriventris* flying we have also found *Phlox* blooming.

Bombylius lancifer kanabensis, n. ssp.

Like *lancifer* O.S. except it has far fewer black hairs on thorax and abdomen. Pale pile of dorsum glistens in reflected light, making the fly appear to shine. Length 8-10 mm.

MALE.— Head black, face shining brown, face and front from some angles lightly brownish gray pollinose, occiput and chin gray pollinose; pile of ocellar tubercle, front, face, antennae, and a few hairs and scales in a patch on occiput near lower corner of eye brown, with a few black intermixed; lower frontal patch black, sparse hairlike tomentum of front pale grayish yellow; pile of chin white, of occiput grayish yellow (same color as that of adjoining thorax). Antennae slender; segment 1 about three times as long as wide; segment 2 same width as first, about as long as wide; segment 3 not quite as wide as first two, its sides nearly parallel, not quite twice as long as first two combined, its style evenly long conical. Proboscis black, about four-fifths as long as head and body combined.

Thorax black, bluish reflections in some lights, pleura thinly gray pollinose over shining surface; pile fairly long and dense, very pale yellowish gray, nearly white on pleura, a patch of dark brown with a few black hairs before the wing extending onto occiput; macrochaetae not strongly developed, nearly same color as pile. Two black hairs on left posterior callus, none on others.

Wings brownish hyaline, anteroproximal third brownish, color evanescent behind; veins brown; basicostal pile black, a few white hairs near base shading to brown along heavy vein; pile of alulae long, very pale yellowish. Halteres brown. Legs yellow, knees, tarsi, and bases of femora brown, first two pairs broadly so; pile of coxae nearly white, of remainder of legs mostly dark brown to black; tomentum nearly white; bristles black.

Abdomen blue black; pile of dorsum long and dense, faintly yellowish (paler than thorax), tufts on hind angles of second, on hind angles of third when viewed from below, and a few hairs on hind margins of second and succeeding segments black; tomentum nearly white, a sparse patch in center of second and fairly dense crossbands on posterior third of third to fifth segments, covering last segments. Pile of venter mostly white, a few black hairs on hind margins of last three segments; sparse tomentum whitish. Genitalia dull black, shading to brownish at tips.

FEMALE.— Much like the male. Less pilose, but much more tomentose than male. Front brown pollinose; pile black; tomentum golden, a few of the pale scales mixed into the lower frontal patch, especially on inner end. Face with a few scattered yellow hairlike scales scattered among pile. Sparse tomentum of occiput pale yellowish, a few black hairs mixed with pale buff pile near vertex, and a few black and dark buff hairs near lower inner corner of eye. Only a few black hairs in dark band before the wing. Posterior two-thirds of mesonotum and scutellum with sparse pale yellow curly tomentum. Wings only slightly paler than in male. Dark part of femora less extensive than in male.

Bristly black hairs in tufts on hind angles of second and third terga similar to male, relatively more bristly black hairs on hind margins of second and succeeding terga. Second sparsely except in middle, and succeeding terga densely tomentose on posterior half of segments and in centers, forming a distinct nearly white median line; anterior half of segment 1 almost bare of tomentum, front of 3 and 4 with sparse tomentum. Most of pile on first three ventral segments white, on succeeding segments mostly black; tomentum pale yellow to white.

Types.— Male holotype and female allotype: Six miles north of Kanab, Kane Co., Utah, 5-VI-1965 (D. E. & L. M. Johnson). Paratypes: 21♂, 12♀ same data.

The type locality, six road miles north of Kanab, on U.S. Highway 89, is in the red sandstone hills of the Vermillion Cliffs area. The flies were on a red sandy sidehill among scattered *Juniperus osteocarpa* and *Artemesia tridentata*. Associated with this species were males of *Lordotus apicula* Coq. The males were hovering and the females feeding between 8:30 and 10:00 a.m.

This series of flies is quite uniform. There is, however, some variation in the amount of black pile on the thorax and abdomen. But even the darkest specimens have very few black hairs. This subspecies is readily distinguishable from the nominal subspecies by this scarcity of black pile, and by the paler color of the pale pile, which in this subspecies is nearly white. On females there may be a few brown to black hairs on occipital orbits near the vertex; tomentum of front may be pale yellow, on the occiput and the thorax in front of the wing there may be no dark pile; there may be no brown on the femora.

Bombylius major Linnaeus

This is the earliest bee fly on the wing in the spring in our area.. It appears as early as mid-March on the edges of the valley floors and in the foothills. We have not done any early collecting in the southern part of the state and have not seen this species in the collections of others from there. We have seen it in collections from Arizona.

Bombylius metopium Osten Sacken

This small species appears shortly after *major* around the edges of the valleys of the northern part of the state. As the season progresses, *metopium*, like several others of its congeners, moves up into the canyons and onto the foothills. We have found it common in only a few places, but it is so inconspicuous that we may easily have overlooked it at other sites where we were not specifically seeking it. The shining white tomentum on the male completely obscures the front; on the female it is found only at the sides of the antennae. The specimens have a gray appearance.

Bombylius lancifer lancifer Osten Sacken

We have collected this species in the mountains above 7,000 feet elevation from May into July. We have found them in the canyons and on northern slopes of practically every mountain range in which we have sought them in the northern part of Utah. We do not know how far south they may be found. Specimens have been examined from Utah, Oregon, and California.

Bombylius montanus, n. sp.

Facial pile and lower frontal patch wholly white; macrochaetae well developed. Length 9-11 mm.

Male.— Head dark brown, densely gray pollinose, face and oral margin yellowish; pile white, a line of dark brown to black hairs on each side of bare pollinose area on frontal triangle between antennae and vertex, some on ocellar tubercle, and upper and outer side of first antennal segment; tomentum of occiput and lower frontal patch at sides above antennae subshining white, a few brown decumbent hairlike scales at junction of inner orbits on upper front. Antennal segment 1 about twice as long as wide; segment 2 about as wide as first, as long as wide; segment 3 about as wide as first two, about twice as long as first two combined, widest at about the middle, tapering evenly thence to blunt tip; style evenly conical. Proboscis brown, about two-thirds as long as body and head; palpi brown, pile yellow.

Thorax brown, dorsum faintly brownish, pleura densely gray pollinose; pile very dense, pale gray and reddish brown on anterior one-third of mesonotum, sparse on posterior two-thirds except along sides; posterior callosities have dense tufts of pile, reddish at base, gray at ends, bordered next to mesonotum with shorter almost black pile. Sparse pile of mesonotum has pale gray pile with hairlike gray tomentum beneath it in two indistinct longitudinal stripes, with a few black hairs intermixed in the darker contrasting brownish pile on the rest of the disc. Pile and tomentum of scutellum like that of posterior mesonotum; most of macrochaetae brown to black, well developed, three or four on notopleura, a number on posterior callosities and along hind margin of scutellum. Pleura with pile moderately dense, yellowish gray on upper half, less dense and white on lower half.

Anteroproximal half of wing brown, somewhat darker along veins, the color evanescent behind, becoming gray hyaline; veins brown, basicostal pile black, a few white hairs at extreme base of wings; pile of alulae dense, long, white. Halteres brown. Legs yellow, knees and tarsi brown; pile and tomentum pale yellowish to white, bristles black.

Abdomen grayish brown, pollinosity almost same color; pile of first three terga pale brownish yellow on sides, nearly white in middle; dark brown to black bristly hairs form single rows on hind margins on outer third of first and across second and third segments and form prominent tufts on sides of second segment, with small tufts on sides of third; pile of rest of abdominal dorsum white, a few black hairs on hind margin of sixth segment; tomentum white, sparse on second and third, moderately dense on succeeding segments, more concentrated on posterior half and middle of second, third, and fourth; pile of venter mostly white, a few black hairs on terminal three segments; sparse tomentum pale yellow.

Genitalia dark brown and reddish, posterior angles of ninth sternite produced into sharply pointed spinelike projections; pile yellow.

Female.— Much like male but less pilose and much more tomentose. Wings almost completely hyaline. Pile of occiput yellowish, that of front sparse, mixed black and white. Front and face densely pale gray pollinose. Dark pile of thorax paler than in male. Halteres paler than in male. Tomentum on abdomen nearly white, appearing pale brownish on middles of second, third, and fourth terga because less dense, rest of tomentum dense; pile mostly white, that on hind margins of segments two to four black and bristly, brown to pale on fifth and following segments, brown tufts on sides of two and three. Pile of first three sterna mostly white, rest mostly black and brown, bristly on hind margins of segments.

Types.— Male holotype: Aspen Grove, Utah Co., Utah, 19-VII-1953 (D. E. Johnson). Female allotype: Pebble Basin, Bannock Co., Idaho, 24-VII-1948 (D. E. Johnson). Paratypes: 1 ♂ same data as holotype; 1 ♂ Strawberry Valley, Wasatch Co., Utah, 10-VII-1969 (on flax and cinquefoil).

In general appearance this species resembles *eboreus* Painter except that the dark of the wings is distinctly brown rather than blackish. However, the strong development of the macrochaetae sets this species apart from all of its congeners in our area. We have seen specimens from Pasadena, California, which may be this species, but more material will be necessary to be certain. Apparent variation shows pile of posterior callosities all pale gray. Slight rubbing destroys distinctive lines on mesonotum. Macrochaetae may be pale.

The holotype and paratype specimens were collected on the Mt. Timpanogos trail about a half mile from Aspen Grove. There were three males and one female alternately hovering and darting about the site, but only two of the males could be captured.

Bombylius abdominalis, n. sp.

Black, pale pile of dorsum mostly yellowish gray. Length 9-12 mm exclusive of proboscis.

Male.— Head black, densely gray pollinose, oral margin yellow shading to black below antennae. Appressed shining white tomentum above antennae leaves center pollinose strip bare except for a very few long white scales. Black erect pile on bare area next to white tomentum. Several rows of black pile below antennae and on facial orbits, dense yellowish white pile on lower face and oral margin. Tuft of black pile on ocellar tubercle, tomentum of occiput white, pile yellowish gray above, white when light reflects off it. Antennae with first two segments quite straight-sided, slightly wider than third; first more than twice as long as second, third about one and one-half times the length of first two combined. Black pile on first two segments. Proboscis about three-fourths the length of body and head combined, black, as are palpi. The latter about one and one-half times as long as the width of the base of the proboscis, pile black.

Thorax and abdomen black with pale pile from third tergite forward yellowish gray, shining almost white in some lights, that of fourth and following tergites white. Dorsum of thorax with pile dense at sides and front third of mesonotum and on scutellum; shorter on rear two-thirds, sparse, with a few black hairs intermixed, and with scattered decumbent fine golden tomentum. Macrochetae yellowish. Sparse black pile on scutellum and post allar callosities.

Wings hyaline except anterobasal fourth cloudy reddish brown, evanescent behind. Basicostal pile white, with black on front edge. Pile of alulae white, dense and long. Halteres brownish with part of knobs paler.

Legs have black femora, tarsi dark yellowish brown. Vestiture white, except spines are black.

Dorsum of abdomen with pale pile bushy, black pile in prominent band on rear of second tergite, narrower band on third and some black pile on rear of other segments. All pile slightly shorter on sides of second and third tergites. All tomentum of abdomen is white; scant on second and third tergites, more dense in center of each segment, giving the effect of a stripe, wider in the white pile, very narrow in the black pile. Fourth and following segments with dense tomentum. Venter of second and third segments with long white pile and dense long hairlike tomentum, following segments with black and white pile scant, and with short white tomentum also not dense, but forming a stripe at center of last three segments. Genitalia very dark, yet not black in color.

Female.— Much like the male. Tufts of black pile on sides of wide upper front and a few fine golden scales on front. Mesonotum with disc back of long pile covered with decumbent fine golden tomentum, more dense on scutellum, where it is arranged with the ends pointing toward center. Abdomnial dorsum much more white tomentose, longitudinal stripe more than twice as wide as on male and more continuous, with diamond-shaped effect on second and third segments. Much less white pile than male on dorsum, sides about same. Venter less pilose, heavily tomentose on second and third sternites, following ones with short tomentum forming a stripe on fourth to sixth, covering seventh. Type with front femora dark, other femora partly so, and tarsi paler than male.

Types.— Male holotype and female allotype: Stansbury Mountain, Tooele Co., Utah, 23-V-1969 (D. E. Johnson). Paratypes: 23♂, 3♀, topotypical, 23-V-1967, 18-V-1969, 23-V-1969; 8♂, Hickman Canyon, Stansbury Mountain, Tooele Co., Utah, 2-VI-1957; 6♂, 11♀ Clover Creek, Tooele Co., Utah, 9-VI-1957; 16♂, Alpine, Utah Co., Utah, 18-V-1954, 24-V-1969 (D. E. and L. M. Johnson); 1♂ Little Mt., Salt Lake Co., Utah, 17-VI-1968. Other specimens have been collected from Lark, Salt Lake Co., Utah, 9-VI-1953.

In addition to variations in size, there may be little black pile on the thorax; knobs of halteres are sometimes mostly dark; three segment stripe of white tomentum on posterior sternites of male faint or not present; some females have completely pale yellowish brown femora.

The description of this species was incomplete at the time of Mr. Johnson's death. He did not record any information about the ecology of the Stansbury Mountains, Hickman Canyon, or Clover Creek areas, which are all within a 10-mile distance on the east side of the Onaqui Mountains. However, the Alpine specimens were collected in the same strip between cultivated fields as *nigriventris* in the foothills of the Wasatch Mountains, and all the other areas are wild habitat at similar altitudes and with similar vegetation.

Bombylius aestivus, n. sp.

Similar to *aurifer* O.S. but has all red femora, and pile of face, front, and pleura pale tawny instead of nearly white. Length 5-7½ mm.

Male.— Dark brown; yellowish gray pollinose on front, face, first and second antennal segments, mesonotum, pleura, first tergum, and venter of abdomen. Antennae black, segment 1 about twice as long as wide; segment 2 about same width, almost round; segment 3 almost twice as long as other two together, not quite as wide, almost parallel sided. Proboscis black, about two and one-half times as long as head; palpi yellow at base, black about half of length, somewhat longer than width of proboscis.

Pile long and shaggy, moderately dense on face, occiput, thorax, and sides of abdomen; color of pile shining pale tawny, somewhat paler on pleura and abdominal venter, with black pile found in a row below lower frontal patch, a few on antennal segments 1 and 2, and sparse tufts of hairs on anterior lateral angles of third and fourth terga. Tomentum hairlike, shining, of about the same color as pile, moderately dense on thorax and abdomen, a dense appressed patch above each antenna. Genitalia pale red.

Legs red, knees narrowly black, tarsi darkening distally; pile and tomentum as on remainder of body, bristles black.

Wings gray hyaline, brown on anterior proximal one-third, color evanescent behind and distally; pile on base of wings and alulae pale tawny, long and shaggy. Halteres brown, knobs pale.

Female.— Very much like the male. Fewer black hairs on face and on anterior angles of abdominal segments than in male. Abdomen relatively broader, more densely tomentose; front with pile and tomentum as in remainder of body.

Types.— Holotype male: Provo Canyon, Wasatch Co., Utah, 14-VIII-1966 (D. E. Johnson). Allotype female: Tryol Lake, Uintah Mts., Summit Co., Utah (no other information, but collected before 1931). Paratypes: 4♂, 1♀ topotypical with holotype.

Some damaged specimens in the collection show some variation in the amount of black pile on the face, on antennal segment 2 and on the abdomen. Some specimens, particularly females, have only a very few black hairs, or even none at all in these places.

This species may be readily separated from *aurifer aurifer* O.S. which may occur in the same area by the red femora and by the darker color of the pile of the face, occiput, and pleura, which in *aurifer aurifer* are nearly white. Cole's *aurifer pendens* has only partially red femora.

Whereas the other species of *Bombylius* in this area are flies of the spring and very early summer, this species is apparently not on the wing until much later in the season and is not in evidence until long after the others have disappeared from even the high country that seems to be home for *aestivus*.

The type locality is in the Wasatch Mountains about one mile southeast of the Deer Creek Reservoir in Provo Canyon. The flies were collected on a north-facing slope in open areas between patches of scrub oak, *Quercus gambeli*, and choke cherries, *Prunus melanocarpa*. They were feeding on *Helianthus* sp. and *Aster* sp. The elevation is between 7,000 and 8,000 feet above sea level. The allotype has only a locality label, but Tryol Lake is a similar ecological habitat in the Uintah Mts. Other species of bee flies common in the area at the same time include *Poecilanthrax signatipennis* (Cole), *P. sackenii* (Coq.), *P. willistoni* (Coq.), *Sparnopolius coloradensis* Grote, *Villa edititoides* Painter, *Aphoebantus mormon* Melander, and *Lordotus gibbus* Loew.

Bombylius lassenensis, new name

At the time *Bombylius pallescens* Johnson and Maughan (1935) was described, we were unaware that Hesse (1938:226) had used the name for an African species. Since our species is a junior homonym of *Bombylius pallescens* Hesse, the new name *Bombylius lassenensis* is proposed as a replacement. This species, collected in Lassen Co., California, is included in the key in this paper, even though it is not from Utah.

Bombylius auriferoides, n. sp.

Black, pile mostly pale yellowish gray; similar to *aurifer* O. S. but with brown halteres. 4.5-10 mm in length exclusive of proboscis.

Male.— Head black, gray pollinose; pale pile faintly yellowish gray, that of ocellar tubercle, antennae, and outer face mostly black; lower frontal patch covered by dense, appressed, shining, nearly white scales which nearly completely obscure the front. Antennal segment 1 about twice as long as wide; segment 2 same width as first, about as long; segment 3 about one and one-half times as long as first two combined, about as wide at its widest part as first two, widest at its basal third; pile of segment 2 mostly pale, that of segment 1 black. Proboscis about half as long as head and body combined.

Thorax faintly grayish pollinose on the mesonotal disc, densely so on pleura; pile long and dense, that on pleura nearly white; short, moderately sparse shining hairlike scales on mesonotum and scutellum. Wings brown on anteroproximal half, gray hyaline behind, color extends to distal end of cell R_1, evanescent behind; veins brown, darker distally; pile of squamae and extreme base of wing pale, rest of pile of costa black. Halteres brown. Legs black, dense tomentum and most of pile pale, a few dark hairs beneath on first and second femora; bristles black.

Abdomen moderately densely pilose, three tufts of black hairs at anterior angles of third, fourth, and fifth terga; tomentum of abdomen of short, curly, appressed hairlike scales, same color as pile. Genitalia brown, members yellowish distally.

Female.— Much like male, somewhat less pilose and more tomentose. Upper half of front and vertex brownish pollinose, very sparsely tomentose; lower half of front gray pollinose and densely pale yellow tomentose in an uninterrupted band between eyes; pile of ocellar tubercle, front, and antennae with black and pale yellow pile, pale pile being mostly on posterior part of tubercle, along orbits, and on upper part of antennae. Wings somewhat paler than in male. Fewer black hairs at sides of abdomen.

Types.— Male holotype and female allotype: Mt. Timpanogos, Utah Co., Utah, elevation 8,600 ft., 30-VI-1957 (D. E. Johnson). Paratypes: Idaho: Bannock Co., 1♂ Lava Hot Springs, 23-VI-1935. Utah: 18♂, same data as types; Utah Co., Utah: 37♂, 18♀ American Fork Canyon; 1♂, 1♀ Provo; 2♂ Aspen Grove; 8♂, 2♀ Payson Canyon. Salt Lake Co., Utah: 1♂ Lambs Canyon; 4♂, 2♀ Parley's Canyon; 28♂, 7♀ Little Mountain. All specimens collected by D. E. Johnson.

In addition to the remarkable range in size, there is considerable variation in some other characters. The color of the halteres varies from rather pale to very dark brown, with the females usually being somewhat paler than males. The color of pile varies from nearly white to distinctly yellowish, particularly on the dorsum of some specimens. The smaller specimens are usually paler than the larger. The very early season flies are usually paler in all respects than later season specimens. The amount of black pile on the sides of the abdomen varies from three distinct tufts in some specimens to only a few inconspicuous black hairs in others. Some males have no black hairs on either the ocellar tubercle or antennae, while others have a few on either or both. There is variation in the number of black hairs on the antennae, front, and ocellar tubercle of the females; but always there are at least same black hairs at all three of these locations, and always there are some pale hairs along the orbits on the lower front. There is some variation in the relative length of the proboscis. The third antennal segment varies somewhat in shape in drying, but always, in both sexes, there is some constriction between the base of the segment and its widest point, which is nearly always at the basal third. Also, this segment is always narrowest just before the tip, flaring more or less to the end where the onion-shaped style is attached.

This species and *aurifer* O. S. are so similar in general appearance that it was not until we were studying a long series of specimens of what we assumed were *aurifer*, from a single locality to determine the intraspecific variation, that we realized we were dealing with more than one taxon, and that the small differences we had noted consistently separated the whole into two distinct groups. Inasmuch as the two forms have sympatric distribution they can only be considered as distinct species. The following characters may be used to separate them: In *aurifer* the halteres are always pale yellow; in *auriferoides* they are some shade of brown; the pile of the vertex and front of the females of *aurifer* is always wholly yellow, while in *auriferoides* it is always mixed black and yellow. The sides of the third antennal segment of *aurifer* females are always nearly parallel for the proximal half, and then evenly tapering to the end; this segment in *auriferoides* is always more or less restricted near the base and before the tip, and the widest part is usually before the middle. The dark color in the wing of the males of *aurifer* does not extend beyond the tip of vein R_1; in *auriferoides* it more or less fills all of cell R_1. The females are more readily separated than the males.

Reexamination of the material listed in the earlier paper by Maughan (1935) shows that all specimens studied are *auriferoides* rather than *aurifer*. The specimens are in too poor condition to include as paratypes. We have found *auriferoides* to be more numerous than *aurifer* in the study area.

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BREEDING RANGE EXPANSION OF THE STARLING IN UTAH

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Abstract.— The discovery and observation of colonies of starlings nesting in the eastern Great Basin desert indicates further expansion of the breeding range of this species in Utah. Data on nest site selection, nesting productivity, food habits, and relationships with other avian species are presented.

The dispersal and establishment of starlings (*Sturnis vulgaris*) in North America has been well documented (Bent 1950; Davis 1960). In Utah information on the initial spread of this species was summarized by Behle (1954). While studying raptor populations in central Utah from 1967 to 1972 I observed several small colonies of starlings nesting in desert habitats. I believe these colonies show the establishment of starlings as members of the breeding avifauna of the central Utah Great Basin desert. As such, they represent a breeding range expansion which reflects the general adaptability of this species.

History of the Starling in Utah

The range expansion of starlings in Utah was initially gradual. Starlings were first observed in the state in February 1939 near Salt Lake City. In the next year small winter flocks were observed in other parts of Salt Lake Valley and a lone individual was reported near Lehi, Utah County. In January 1941 a flock of 200 was observed at Mt. Carmel, Kane County, in south central Utah (Behle 1958). From 1941 to 1947 small winter flocks were frequently observed near feedlots and ranches in Salt Lake Valley. In 1948 their winter range again expanded; a flock of 1,000 individuals was seen northward in Davis County; and a single individual was found in Kanab, Kane County. Their winter range expansion continued in 1950, when they were recorded for the first time northward in Box Elder County and westward in Tooele County. During the decade 1950-1960 winter flocks of starlings increased tremendously. Bailey (1966) reported flocks as large as 100,000 and noted that they constituted an important agricultural pest of feedlots and orchards in 16 counties of the state, from Washington County in the south to Box Elder County in the north.

The first nest of the starling in Utah was found on 25 May 1949 in an old woodpecker or flicker hole on the west side of Salt Lake City. In the following year a nest was discovered in a shed at Randolph, Rich County (Behle 1954). Within six years starlings were nesting at many localities in the central, populated valleys of the state. In 1956 a starling nest containing young was found in a shed at Lynn, in the northwestern corner of the state (Behle 1958). Starlings have since spread throughout most of the state and now are a sizable component of the breeding bird populations of the towns, settlements, and ranches of the northern Great Basin area (Hayward 1967). During my study of raptor populations in Cedar Valley, Utah County, and Rush Valley, Tooele County, I found starlings and house sparrows (*Passer domesticus*) to be the most common breeding birds in small towns such as Fairfield and Cedar Fort. In these settlements they typically nested in a variety of buildings and in holes in cottonwoods and willows. They were also frequently observed nesting in wind breaks bordering agricultural fields and pastures. Here they usually nested in holes in living and dead trees, but unused bulky stick nests of hawks and magpies (*Pica pica*) were also appropriated. My observations in other settled areas of Tooele, Juab, and Millard counties showed similar choices of nesting site selection and habitats by starlings.

I believe that my observations of starlings nesting in desert habitats warrant particular interest because this suggests invasion and adaptation to a new habitat as well as a further range extension by this species in Utah.

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Nesting Localities and Nest Sites

I observed nine breeding sites located in three counties, all judged to be examples of a starling breeding range expansion into habitats of the northern Great Basin desert. It should, however, be mentioned that each spring and summer I frequently observed starlings in additional localities, and the breeding range expansion of this species is undoubtedly occurring over a much wider area than my records indicate. Four of the nine sites supported small but regular breeding populations during the six-year study. The other sites were irregularly active.

Starlings displayed their well-known adaptability in choosing nest sites (Kessel 1957), and a comparison of nesting habitats and nest site selection indicates some degree of opportunism. Although Michael (1971) considered his observations of starlings nesting in rocky cliffs in Kentucky and West Virginia to be significant, I found 18 of 42 (42.9 percent) of the nests I actually located to be placed in crevices in the sheer walls of quarries and cliffs. Of the remainder, 9 (21.4 percent) nests were located in some type of abandoned mining structure, 8 (19 percent) were found in holes in junipers (*Juniperus osteosperma*), and 7 (16.7 percent) in stick nests of hawks, owls, and ravens (*Corvus corax*). The choice of nesting sites reflected the diversity of the nesting habitat. Usually pairs of a colony were found nesting in a variety of sites where available.

Several sites will be described in some detail to facilitate comparison with possible future breeding locations.

Utah County.— Five sites were found, all in the western section of the county.

A colony was located in the vicinity of an abandoned mine and clay pit operation at Five Mile Pass, which is about six miles west of Fairfield. The habitat at this locale is desert scrub intermixed with widely scattered junipers. Four mine structures are still standing and there are six large quarries and clay pits. From 1967 to 1972 a total of 17 nests were found at this site as follows: 2 in 1967; 4 in 1968; 5 in 1969; 3 in 1970; 1 in 1971 and 2 in 1972. Several additional pairs were seen each year after 1968, and some may have been nesting. Of the nests found, seven were placed in crevices in the rock walls of clay pits, four in holes in junipers, three in the walls of a mine shack, two in mine bunkers, and one in the beam supports of a mine tunnel.

A second colony active during all six breeding seasons was located in the vicinity of the abandoned Little Topliff quarry at Ten Mile Pass. This site was approximately 14 miles southwest of Fairfield and 5 miles northwest of Allan's Ranch. The habitat of this site is a mixture of grasses and desert scrub. Fourteen nests were found at this site: 2 in 1967, 2 in 1968, 5 in 1969, 3 in 1970, 1 in 1971, and 1 in 1972. Again, additional pairs were observed each year after 1968. Eight of the nests were located in crevices in the sheer rock face of the quarry, two in an unused golden eagle (*Aquila chrysaetos*) nest, one in an abandoned prairie falcon (*Falco mexicanus*) nest, and three in cracks in a wooden retaining wall.

Another Ten Mile Pass site was located in the abandoned Big Topliff quarry which is about one mile east of Little Topliff. This quarry, one of the largest in the area, is bordered entirely by desert scrub communities. Two nests were found in 1970, both constructed in an unused golden eagle nest. Several individuals, some of which may have been paired, were observed in 1971.

In 1969 a third colony was found at Ten Mile Pass, about two miles east of Big Topliff quarry and three miles northwest of Allan's Ranch. Several individuals and two nests each were found in 1969 and 1970 in a large limestone cliff line 400 feet above the valley floor. The surrounding habitat is sparse desert scrub devoid of trees.

Three of the four nests were located in crevices in the cliff face. The fourth was in an unused red-tailed hawk (*Buteo jamaicensis*) nest constructed in a large crevice.

A fifth colony was found in the vicinity of the abandoned Tintic Empire Mine, located in the foothills of the Boulter Mountains approximately four miles north of Eureka and two and one-half miles southeast of Allan's Ranch. The surrounding habitat of this colony was a large stand of widely spaced junipers. Two nests, both located in holes in junipers, were found in 1969; other pairs were present. Only one bird was seen when this site was rechecked in 1970, and none were observed in 1971. I was unable to visit this site during the 1972 breeding season.

Tooele County.— I found nests at two separate sites in this county and evidence of nesting activity at one additional site.

In 1968 and again in 1969 I found a starling nest in a hole in a juniper near the entrance to Black Rock Canyon. This nest site was approximately seven miles east of Vernon. This site was unusually interesting because it was located in a juniper which also supported an active great horned owl (*Bubo virginianus*) nest during the two nesting seasons. Both starling and great horned owl nesting attempts were successful during the two nesting seasons. No nest was present in 1970 or 1971, but starlings were observed in May and June in the same juniper stand, although about one-half mile above the original nesting site.

On 15 June 1969 I observed several starlings in a juniper stand in the northern foothills of Simpson Mountains. This site is approximately 16 miles northeast of Simpson Springs. One nest was found in a hole in a juniper, and, judging by the behavior of the other birds, additional nests may have been present.

Juab County.— Murphy et al. (1969) observed 12 starlings near a golden eagle nest located in sandstone cliffs at Yuba Dam State Park and presumed them to be nesting.

On 15 May 1970 a pair of starlings was observed approximately six miles north of Trout Creek in the foothills of the Deep Creek Mountains. One carried nesting material and was seen in the vicinity of a small stand of junipers. We were, however, unable to locate a nest.

Reproductive Chronology and Success

Starlings were not found in the vicinity of the desert nesting sites during the fall and winter months (September through February), although small flocks were frequently observed in nearby settlements. They began appearing in the future nest site vicinity in early March, and the majority were present by late March and early April. During this time they were frequently seen inspecting dilapidated mine buildings and holes in junipers and often reacted to my presence near these sites by protesting vigorously.

Adults carrying nesting material were seen in late March and throughout April. Most nests were constructed of grass, primarily wheat grass (*Agropyron spicatum*), and frequently lined with feathers. Four of the nests I found were decorated with juniper greenery.

Nests containing eggs were found from late April through mid-June. Dates of the 24 nests with eggs which we found are as follows: 27, 30 April; 1, 2, 4(3), 10 (2), 17(4), 19, 21(2), 30 May; 4, 9(3), and 19 June. I found no evidence of attempts to raise a second brood in July and August.

The clutch size of these nests averaged 4.2 ± 1.2 eggs (range, 3-7; mode, 4). A clutch size comparison with other areas is presented in Table 1. Utah clutch size averaged significantly smaller than those of New York and Holland ($t=3.95$, 2.84 respectively; $P<0.05$ for both) but not significantly different from northwestern England ($t=1.5$, $P>0.90$).

Young were in the nest from mid-May through mid-July. My earliest and latest dates for nests with young are 14 May and 28 July. The brood size of 17 nests was 3.9 ± 1.1 young (range, 2-7; mode, 4). Interestingly, there was no significant difference among brood sizes of Utah,

Table 1. Clutch and brood size comparison of central Utah nests.*

Location	No. clutches	No. eggs per clutch	No. broods	No. young per brood	Author
Central Utah	24	4.5 ± 1.2	17	3.9 ± 1.1	Present Study
Ithaca, New York	199	5.5 ± 0.9	230	4.3 ± 1.3	Kessell (1957)
Holland	1592	5.2 ± 1.0	1377	4.4 ± 1.3	Kluijver (1933)
NW England	105	4.9 ± 1.1	913	4.2 ± 1.1	Lack (1948)

*Data is average ± one standard deviation.

New York, Holland, and England nests, indicating perhaps a somewhat higher overall hatching success of Utah nests.

Overall reproductive success was high. Of 13 nests on which I was able to obtain complete information, 12 successfully hatched young; and of these, 11 nests fledged young. Two nests were abandoned; one containing three eggs and one with five young. Neither pair attempted to renest. Overall hatching and fledging success was 94.2 percent and 84.6 percent, respectively. Both percentages are slightly higher than reported from previous studies in other areas.

Foraging and Food Habits

Information on foraging and food habits is limited and was obtained from morning observation of three nests, two in 1969 and one in 1970, all located in the Five Mile Pass nesting colony. Adults were observed from a parked vehicle with a 40X spotting scope attached to a window mount. Only those food items brought to the nest site which could be identified are included in the results presented in Table 2.

Adults foraged predominantly in the sagebrush-wheatgrass (*Artemisia-Agropyron*) associations which were the common plant communities in the nesting site vicinities. They spent considerably less time in the ground layer vegetation of pinyon-juniper (*Pinus-Juniperus*) communities and among the rubble-strewn floor of quarries.

Over 86 percent of the arthropod food items brought to the nest were insects. Of these, Orthoptera comprised 56 percent and Coleoptera almost 27 percent. Araenids were the only other animal food which was taken in significant quantities. In a food habit study in eastern Texas based on stomach contents, Russell (1967) found Orthoptera and Coleoptera, particularly Carabidae, to comprise 84 percent of the total insects eaten and 68 percent of the total food, with other arthropods and some plant material constituting the remainder of the diet. I did not identify any utilization of plant material for food, but results are undoubtedly biased because the small nesting populations precluded collection of adults and young for stomach contents analysis. Both Killpack and Crittenden (1952) and Bailey (1966) noted the extensive use of such plant materials as grain and corn silage by wintering flocks of starlings. Starlings are undoubtedly opportunistic in their feeding habits and utilize the most available food. This is reinforced by a comparison of the food habits of these desert nesting starlings with the result of Fautin's (1946) investigations of the invertebrate populations of the sagebrush community. Analysis reveals that, with the exception of Formicidae, starlings utilized the most prevalent ground layer invertebrates in the sagebrush community.

Table 2. Arthropod food of starlings in the eastern Great Basin.

Item	No. indv.	% Freq.
Acrididae	31	47.0
Tettigoniidae	6	9.1
Carabidae	11	16.7
Tenebrionidae	3	4.5
Scarabidae	3	4.5
Cicadellidae	2	3.0
Formicidae	1	1.5
Araneidae	9	13.6
Totals	66	99.9

Relations with Other Species

Starlings appear to be the predominant avian species in the vicinity of their breeding locales. Other birds observed in the same locale included the house sparrow, pinyon jays (*Gymnorhinus cyanocephala*), scrub jays (*Aphelocoma coerulescens*), mourning doves (*Zenaidura macroura*), common nighthawks (*Chordeiles minor*), and mountain bluebirds (*Sialia currucoides*). Only house sparrows were common nesting associates, and at two sites, Big and Little Topliff quarries, they outnumbered the starlings. At these and other sites the two species appeared to mutually tolerate one another and no aggressive interactions were observed. We did observe starlings interacting aggressively with scrub jays (twice) and mourning doves (twice) which had perched in the immediate vicinity of the nesting site. In each instance the starlings displaced the intruding birds. The only direct evidence of nest displacement which we observed concerned a mountain bluebird nest which contained six eggs when discovered on 15 May 1970. When this nest was rechecked five days later we found an adult starling sitting on a clutch of six eggs. No trace of the mountain bluebird was found, and the adults were not observed again in the nesting territory.

In a previous study of the food habits of raptors breeding in the eastern Great Basin Desert, starlings were occasionally recorded as prey of several hawk and owl species (Smith and Murphy 1973). It is possible that their plumage, size, and aggressive habits make them conspicuous targets and hence more liable to be preyed upon by raptors.

Discussion

Within the relatively short time span of 30 years the starling has become a predominant component of Utah's avian fauna. Its successful invasion and establishment can be roughly delineated into three segments, each of approximately 10 years duration. In the first 10-year period (1939-1948) following their appearance in the state, starlings were observed only as individuals or small flocks of winter visitants. In the next 10 years (1949-1958) these winter flocks increased tremendously in size and greatly expanded their winter range to include most of the populated central portions of the state. The first nesting attempts were reported early in this period and by the end of the decade small nesting populations were found in many widely separated towns and settlements of the state. In the third 10-year period (1959-1968) both winter and summer starling populations had increased in size to the point at which the starling had achieved the status of a major pest species. During this time the starling became (with the possible exception of the house sparrow in some areas) the most abundant bird throughout most of the settled portions of the state. Although most common in cities and towns, they were also found in widely separated settlements and ranches. In winter they formed large flocks which, through their feeding and roosting activities, became an economic nuisance to feedlot owners and fruit growers throughout the state.

At the present time, so far as is known, starlings nest in all the settlements and towns in the state and have recently extended their breeding range into desert habitats. Although initially sporadic, their occupation of distinctly desert habitats for nesting purposes has recently become more widespread, suggesting that they have been able to adapt to a new habitat type.

In analyzing the range expansion and establishment of starlings in Utah I consider the following to be of significance: (1) mobility, (2) suitable climate, (3) suitable habitat, and (4) sufficient population pressure. The four factors are, in fact, a measure of the starling's adaptability and, when considered together, explain the success of this species. Although not specifically investigated in this study, their rapid range expansion across North America indicates that starlings have adequate powers of mobility and wide climatic tolerances. While largely nonmigratory, their behavorial adaptation of forming large, mobile winter flocks which break up and disperse to favorable nesting areas in spring undoubtedly allows some exploratory activity which may in turn lead to further range expansion.

Water, but not food, may pose the only potential limiting factor for starling range expansion into the Great Basin desert. Starlings at their desert breeding sites were observed drinking water from ephemeral rain puddles and from livestock watering troughs.

The adaptability of starlings to new habitats is well known (Kessell 1957). A review of the pattern of starling invasion in Utah suggests that a habitat with some form of human modification provides a favorable impetus for range expansion. Thus, widely separated towns and settlements were occupied within 20 years, but the intervening areas of desert were not invaded until after starling populations were well established in nearby settlements. Only after starling populations had occupied these locales did a further range expansion into the upper Great Basin desert take place. It is quite possible that the human habitats provided breeding sites, probably due to the well-known breeding behavior adaptations of this species with reference to man, which resulted in local population increases. Pressures resulting from these local population increases may have encouraged starlings to examine the adjacent habitats of the upper Great Basin desert.

The short time span of their successful utilization of this new habitat suggests behavorial adaptations rather than genetic changes within the population. However, the possibility of future evolutionary changes in populations occupying such habitats may warrant further study.

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SOME PARASITES OF PADDLEFISH (*POLYODON SPATHULA*) FROM THE YELLOWSTONE RIVER, MONTANA

Lawrence L. Lockard[1] and R. Randall Parsons[2]

Abstract.— One species of copepod (*Ergasilus elongatus*), one trematode (*Diclybothrium hamulatum*), two nematodes (*Camallanus oxycephalus* and *Contracaecum* sp.), and two cestodes (*Marsipometra hastata* and *M. parva*) were recovered from 17 paddlefish (*Polyodon spathula*) collected from the Yellowstone River, Montana, on 11 and 18 May 1973. The male paddlefish averaged 69.4 nematodes and 157.6 cestodes per infected fish while the females averaged 12.0 nematodes and 415.7 cestodes. The higher intensity of cestode infection in female paddlefish was attributed to their larger size and consequent greater intake of food resulting in more exposure to the cestode intermediate hosts (*Cyclops bicuspidatus*).

There have been relatively few reports on the parasites of paddlefish (*Polyodon spathula*). Linton (1898) found tapeworms in paddlefish from the Ohio River, Ohio. Stockard (1907) mentions large numbers of cestodes in paddlefish from the state of Mississippi; and Wilson (1914) found parasitic copepods on paddlefish from the Mississippi River in Illinois and Iowa. Simer (1929 and 1930) and Beaver and Simer (1940) examined 171 paddlefish from the Tallahatchie River, Mississippi, and reported on trematodes and cestodes from them. Bangham and Vernard (1942) found one paddlefish from Reelfoot Lake, Tennessee, infected with trematodes, nematodes, and cestodes. Meyer (1946) discovered leeches parasitizing paddlefish while Causey (1957) examined one paddlefish and found parasitic copepods. Meyer (1960) studied cestodes from paddlefish collected from the Mississippi River in Iowa and the Missouri River in South Dakota. Hugghins (1972) examined one paddlefish from Fort Randall Reservoir on the Missouri River in South Dakota and found it parasitized with tapeworms and nematodes. Weisel (1973) reported unidentifted tapeworms and nematodes from 3 paddlefish from the Yellowstone River, Montana. The present study was undertaken in an effort to gain information on the parasites of paddlefish from Montana.

Methods

This report was based upon the necropsy of 17 paddlefish collected from the spawning run in the Yellowstone River near Intake, Montana, on 11 and 18 May 1973. The fish were eviscerated, and the viscera and gills were placed in plastic bags and frozen for later examination. The gastrointestinal tract was dissected, and the contents were washed onto a 200-mesh screen, then transferred to an illuminated tray (Barber and Lockard 1973) for examination. Cestodes were fixed in AFA (alcohol-formalin-acetic acid) and stained with Delafield's hematoxylin. Nematodes were placed in a mixture of 70 percent alcohol and 5 percent glycerine and later mounted in glycerine. The liver, heart, gall bladder, spleen, and gills were dissected and each was placed in a jar with water and agitated on a mechanical shaker for 5-10 minutes. The contents were poured onto a 200-mesh screen, washed, transferred to an illuminated tray, and examined. Trematodes and copepods were placed in a mixture of 70 percent alcohol and 5 percent glycerine. The ovaries, testes, and gas bladder were examined grossly and observed abnormalities checked microscopically.

Results

The ten male paddlefish had an average weight of 10.6 kilograms and range of 6.8 to 13.6 kilograms, while the seven females had an average weight of 22.8 kilograms and range of 20.0 to 27.2 kilograms.

Table 1 lists the rates of infection with copepods, trematodes, nematodes, and cestodes recovered from paddlefish during this study. The parasitic copepod *Ergasilus elongatus* was identified by Dr. Z. Kabata of the Fisheries Research Board of Canada. The trematode *Diclybothrium hamulatum* was identified by Dr. Fred P. Meyer of the Bureau of Sport Fisheries and Wildlife. Identifications of the nematodes *Camallanus oxycephalus* and *Contracaecum* sp. were confirmed by Dr. E. J.

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TABLE 1. Incidence of parasites of *Polydon spathula* collected from the Yellowstone River, Montana.

Parasite	Percent infected		Mean no. of parasites (range)	
	Male	Female	Male	Female
Ergasilus elongatus	30	14		
Diclybothrium hamulatum	100	100		
Camallanus oxycephalus	80	86	69.4 (12-302)	12.0 (4-25)
Contracaecum sp.	80	86		
Nematode cysts	100	100		
Marsipometra hastata	100	100	157.6 (34-356)	415.7 (37-1013)
M. parva	90	100		

Hugghins of South Dakota State University and Dr. G. L. Hoffman of the United States Fish and Wildlife Service, respectively. Spherical cysts (1-3 mm in diameter) containing larval nematodes were present on the surface of the stomach, pyloric caecum, and the intestine of all fish examined. All 17 paddlefish examined were infected by tapeworms identified from Beaver and Simer (1940) and Meyer (1960) as *Marsipometra hastata* and *M. parva.*

DISCUSSION

It was felt that the handling procedures greatly reduced chances of discovering parasitic copepods as well as monogenetic flukes which may have been present on the gills of the fish. Causey (1957) says statements of incidence of infection for copepods have little value. Thus, the incidence of infection of copepods found in Table 1 may not be indicative of the number of infected fish actually present. Likewise, quantitative analysis on the presence of the monogenetic fluke would be of little value.

Differences in intensity of nematode infections (Table 1) between male and female paddlefish were noted but were difficult to interpret because of the presence of immature *Contracaecum* sp. in the intestine.

Simer (1930) and Beaver and Simer (1940) name three species of cestodes infecting paddlefish: *Marsipometra hastata*, *M. parva*, and *M. confusa*. Meyer (1960) examined tapeworms from these studies and his own material and concluded that *M. hastata* and *M. confusa* were synonymous. He also found *Cyclops bicuspidatus* to be the intermediate host of *M. hastata*. In this study no attempt was made to distinguish *M. confusa* from *M. hastata*. Females had a higher intensity of tapeworm infection than male paddlefish, and this may be attributable to larger size of the females. Females weighed more than twice as much as males and thus would have ingested more of the intermediate hosts of these parasites while feeding.

ACKNOWLEDGMENT

The authors express their appreciation to Jeffrey Bagdanov for assisting with the necropsy of the paddlefish.

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REPRODUCTIVE CYCLE OF THE BELDING GROUND SQUIRREL (*SPERMOPHILUS BELDINGI BELDINGI*): SEASONAL AND AGE DIFFERENCES

Martin L. Morton[1] and John S. Gallup[2]

Abstract.— The reproductive cycle in Belding ground squirrels was studied in the Sierra Nevada Mountains at two locations, one at 2,100 m elevation, the other at 3,000 m.

Adults emerged from hibernation completely prepared physiologically for reproduction. Males tended to emerge slightly ahead of females and yearlings tended to emerge later than adults. Yearling females were fertile but produced smaller litters than adults, 4.48 vs. 6.31. Yearling males were infertile. They exhibited a slight seasonal cycle in testicular growth but did not reach sexual maturity. Testicular growth and spermatogenesis were incipient in many adults and in yearlings prior to hibernation.

Hibernation and seasonal breeding are important survival strategems of rodents living at high latitude or high altitude. Typically in these environments there are extreme seasonal oscillations in ambient conditions. Winters tend to be long and cold and summers brief and sharply delimited. Dormancy is employed as a means of bridging the long gap of energy shortage in winter, and breeding is coincident with the clement weather and abundant food of summer. Both responses require advance preparation and accurate timing to be maximally adaptive. The physiology of hibernation is currently a viable, active field of study, whereas seasonal breeding has aroused less interest and its complexities, especially in wild populations, are poorly understood (Chapman 1972).

Herein we report on seasonal changes in reproductive functions of the Belding ground squirrel (*Spermophilus beldingi beldingi*), a hibernator that lives at high altitude in the Sierra Nevada Mountains of California.

Methods

This study extended from 1969 to 1973 and was on *S. b. beldingi* living principally in meadows of Lee Vining Canyon, Mono County, California. A number of squirrels were live-trapped or shot at Big Bend (elevation ca. 2,100 m), but most data are from those living near Tioga Pass (elevation ca. 3,000 m). At both areas we carried on an extensive mark-release program throughout the time squirrels were active above ground. This program enabled us (1) to follow seasonal changes in body weights and dimensions and external appearance in individuals of known age and (2) to collect animals of known age for specimens.

Live-trapping was conducted with Tomahawk wire mesh traps baited with peanut butter. A few specimens were collected with a .22 caliber rifle. Animals trapped for the first time were toe-clipped in a standard pattern never involving more than one toe per foot. All animals were examined externally for appearance of vulva and mammae or of scrotal pigmentation and position of testes.

Freshly excised reproductive organs were fixed in Bouin's solution and transferred to 70 percent ethanol. At the time of transfer they were debrided, blotted, and weighed to the nearest 0.1 mg. Tissues were sectioned at 7 or 10μ and stained with hematoxylin and eosin. Measurements of seminiferous tubules were taken with an ocular micrometer.

Results

Arousal schedule.— The sequence and pace of events in the active season were alike at the two study areas, but the active season at Big Bend usually began at least six weeks in advance of that at Tioga Pass. Snowcover was not comparable at the two sites at the beginning of the season. At Big Bend most burrow sites were clear of snow when emergence occurred. At Tioga Pass emergence tended to begin on knolls that were the first areas to become snow free, but many individuals tunneled out at sites covered by snow up to a depth of 2 m. Similar effects of snowpack on emergence of *S. columbianus* were noted by Shaw (1925). There was considerable annual variation in snow conditions and the schedule of *S. b. beldingi* was affected accordingly (see beyond).

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Adult males were the first animals seen above ground at a given location, but a few adult females and an occasional yearling could be found within a few days thereafter.

Testes.— At emergence adult males had scrotal testes weighing about 2 to 3 g, the maximum weight seen during the entire active season (Fig. 1). The scrotum was darkly pigmented. Within a month after emergence testicular weight of adults began to decrease noticeably and testes had become inguinal or abdominal in position and scrotal pigmentation was decreasing. Six weeks after emergence testicular weight had decreased to a seasonal minimum that was maintained thereafter at Big Bend until onset of hibernation (Fig. 1, upper). At Tioga Pass, however, considerable increase in testicular weight of adults occurred during the last few weeks of the season (Fig. 1, lower).

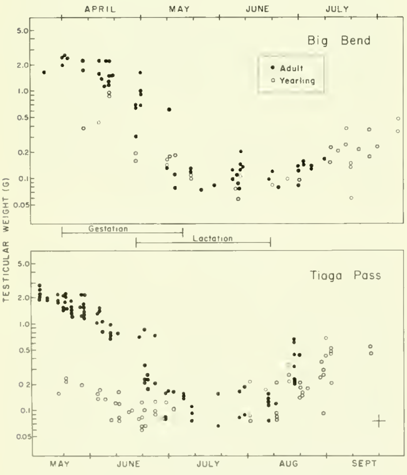

Fig. 1. Paired testes weights of *Spermophilus beldingi beldingi* throughout the active season at two study areas. Note log scale on ordinate. Cross on lower right corner of Tioga Pass data indicates mean testicular weight of juveniles prior to hibernation.

In histological perspective, testes of adults showed intense spermatogenic activity from time of emergence through onset of weight collapse. During this time seminiferous tubules were of large diameter (150 to 250μ) with spermatozoa filling the lumina. As testicular weight decreased spermatogenesis ceased and tubule diameter decreased. During June at Tioga Pass, for example, diameters went from about 150 to 60μ. Beyond June, lumina in seminiferous tubules were absent. Recrudescing testes of adults collected in late August at Tioga Pass had a thickening germinal layer with numerous primary spermatocytes and a few secondary spermatocytes present. Seminiferous tubules had enlarged slightly to a diameter of 80 to 100μ.

Yearling males tended to emerge later than adult males, were of smaller body size (Morton and Parmer, in press), and had considerably smaller abdominal testes (Fig. 1). This was most clearly observed at Tioga Pass where we had a larger pool of marked animals to collect from. Testes of yearlings were about three times heavier at emergence than when they entered hibernation the previous fall as juveniles. A decrease in testicular weight occurred soon after emergence, followed by an increase toward the end of the season.

Two yearlings collected at Big Bend on 18 April 1973 had paired testes weighing 920 and 940 mg. Seminal vesicles of these animals were 37.4 and 34.2 mg, respectively. Although well above resting level, neither set of glands approached those of sexually active adults in weight or cellular maturation.

There was some evidence of a cycle in spermatogenic activity in yearling testes in that a few spermatocytes were produced early in the season. Diameter of seminiferous tubules remained small (below 100μ) throughout the season, and no advanced stage of spermatogenesis was found in any yearling testis. As in adults at Tioga Pass, tubule diameter increased slightly in concert with increased testicular weight, and spermatocyte numbers increased just prior to hibernation.

Seminal vesicles.— Seminal vesicles of adults tended to increase in weight for a few days following emergence, remained at maximum size for a few weeks, then decreased to minimum size for the rest of the season (Fig. 2). These glands were only slightly enlarged in yearlings early in the season and tended to decrease in weight thereafter. As shown in *S. lateralis* by McKeever (1964), seminal vesicle growth is controlled by testicular hormone. The near-maximum size of seminal vesicles in recently emerged *S. b. beldingi* suggests that upon final arousal they have fully secretory testes.

In microscopic appearance the heaviest seminal vesicles of adults had a distended mucosal epithelium and lumina filled with seminal fluid in a colloidal state. As involution occurred the colloid disappeared, the mucosal layer became shrunken and folded, and the lumina nearly disappeared. This appearance was maintained through onset of dormancy. Seminal vesicles of yearlings were without detectable cellular change throughout the active season.

SEXUAL CYCLE OF FEMALES.— Adult females appeared to be sexually receptive almost immediately after emergence as judged by their swollen, open vulvae and enlarged, turgid uteri. Copulation was never observed, but additional evidence that mating occurred soon after emergence is that a few adults were already lactating during the fifth week after the first active females were seen. Gestation period in *S. beldingi* is thought to be 27 to 31 days (Turner 1972).

Yearlings were in estrous later in the season than adults because they tended to emerge later and because estrous appeared to be delayed in smaller yearlings until additional body growth had occurred.

Seasonal changes in ovarian weight were about two-fold and were similar for the two age groups. For the first six weeks after emergence ovaries weighed 20 to 30 mg. Weight then decreased to 8 to 15 mg for the remainder of the season.

Anovulatory follicles and corpora lutea tended to enlarge during gestation and reached maximum diameters at parturition. These structures shrank in postpartum females. By the end of lactation follicular cavities were much reduced or absent and corpora lutea were becoming indistinct. No ovarian recrudescence was observed in yearlings or adults prior to hibernation, but follicular enlargement began in juveniles during their last weeks of activity after older animals had already become dormant.

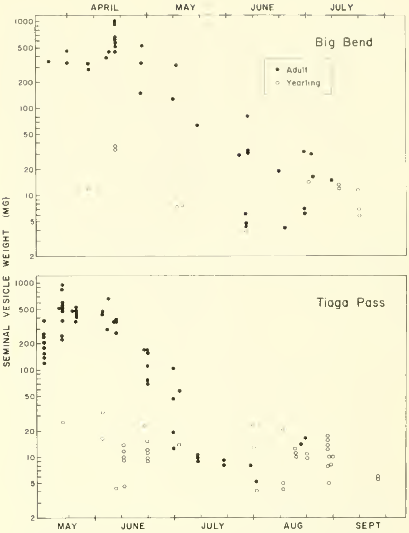

Fig. 2. Paired seminal vesicle weights of *Spermophilus beldingi beldingi* throughout the active season at two study areas. Note log scale on ordinate.

Emergence of females at Tioga Pass occurred over a span of several weeks. As a result parturition dates were spread out and the percentage of females lactating at a given time was almost never 100 percent (Fig. 3). As far as we know, all females reproduced, although some of the smaller yearlings collected in late June at Tioga Pass had unscarred, thin, virgin-like uteri. Note that testicular atrophy was well advanced in adult males at that time (Fig. 1, lower). It is possible that a few yearling females did not bear young. Another possibility is that implantation was delayed in those of small body size. There are indications in other studies that female *Spermophilus* may become impregnated well after testicular collapse has begun in males (Wells 1935; Tomich 1962; McKeever 1966).

If these smaller females do have young, they will be born relatively late in the season (we have observed considerable disparity in size of juveniles at the end of the season; Morton, Maxwell, and

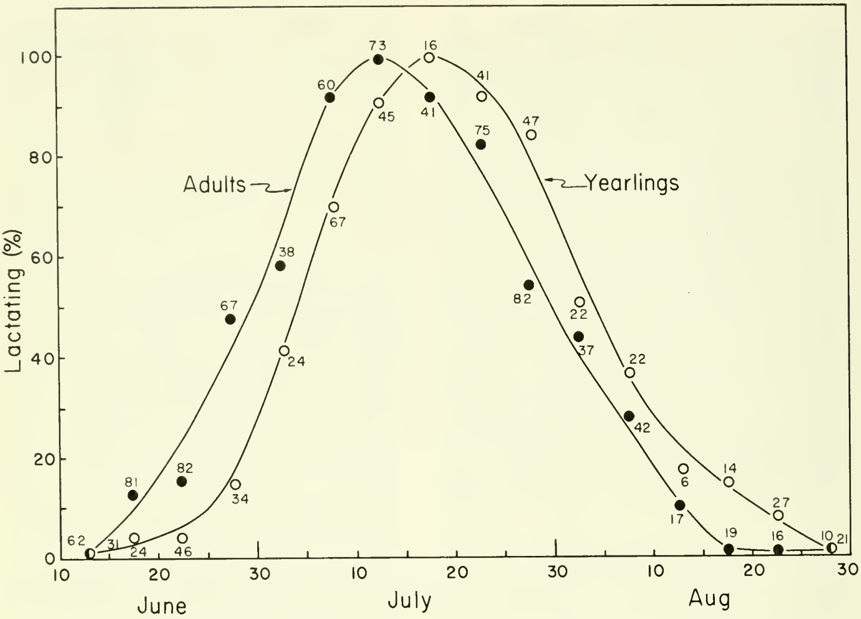

Fig. 3. Mean percentage of female *Spermophilus beldingi beldingi* thought to be lactating at specific 5-day intervals at Tioga Pass. Numerals indicate sample sizes.

Wade 1974), and if these young survive, a self-perpetuating cycle of late reproduction by small yearling females will have been established.

Litter size.— Our specimens and records of frequently retrapped females indicate that they have one litter per season. This was true even of the earliest females to breed. We obtained measurements of litter size through counts of placental scars and implanted embryos in collected specimens and through litters born in captivity (Table 1). The difference in means between counts of scars and of embryos was not different according to a *t* test (P> 0.05) but some prenatal loss did occur. Ten of the 228 embryos examined (4.4%) were partially reabsorbed. This is similar to the reabsorption rate found in *S. lateralis* (McKeever 1964; Skryja and Clark 1970) and in *S. richardsonii* (Sheppard 1974). The lowest estimate of litter size was obtained from births in captivity. Cannibalism of their young by confined females was noted in a few cases but all cases may not have been detected.

Table 1. Measurements of litter size in *Spermophilus beldingi beldingi*.

	Mean	S.D.	N
Placental scars			
Adults	6.88	1.22	17
Yearlings	5.00	....	2
Implanted embryos			
Adults	6.33	2.01	21
Yearlings	4.75	1.07	20
Young per captive			
Adults	5.71	1.45	17
Yearlings	4.00	1.00	5
Total, all measurements			
Adults	6.31	1.67	55
Yearlings	4.48	1.40	27

When all measurements were summed, mean litter size of adults (6.31) was significantly larger (P< 0.01) than that of yearlings (4.48). This is quite similar to age differences in litter size observed in *S. armatus* (Slade and Balph 1974).

Discussion

In most published reports there is little indication that yearling *Spermophilus* of either sex are functionally or visually separable from older animals (compare Mayer and Roche 1954; McKeever 1963, 1964; Carl 1971; Zimmerman 1972), although they may constitute a considerable portion of the breeding population. However, yearlings engage in unique behavioral interactions with older animals as they are integrated into the community of reproducers (Michener and Michener 1973) and should be the focus of more study. Even in the larger-bodied sciurids such as *Marmota monax* (Christian, Steinberger, and McKinney 1972) and *Cynomys leucurus* (Bakko and Brown 1967) some males are sexually mature as yearlings.

The lack of reproductive capacity in yearling male but not in female *S. b. beldingi* is an interesting contrast that indicates the operation of sex-specific selection factors. As pointed out by Conaway (1971) the nonpregnant cycle is a rarity and cannot be afforded by most natural populations. The breeding season is delayed slightly in yearling female *S. b. beldingi* by their emergence schedule and the apparent necessity for some to attain greater body size before pregnancy. Nevertheless, all or nearly all do reproduce. In males, however, there is greater total body size to be reached than in females (Morton 1975) and selection seems to have favored the strategy of diverting energy expenditure from reproductive activities toward growth. Indeed from the last half of the yearling season onward males are significantly larger than females (Morton and Parmer, in press). We have additional evidence that delayed sexual development in male *S. b. beldingi* is tied directly to body size. Two males born in captivity and kept under classroom conditions for display became excessively obese in their first autumn, went through bouts of estivation for several months, and possessed scrotal testes soon after resuming normothermia at about nine months of age.

Growth rates of captive *S. b. beldingi* juveniles are comparable to those of other hibernatory *Spermophilus*, but there are indications that growth is much slower in feral animals than in captives even before weaning (Morton and Tung 1971). It may be that it is unusually difficult for *S. b. beldingi* living at high altitude to achieve adult size and reproductive potential simultaneously. We have suggested (Morton and Tung 1971) and now shown clearly (Morton and Parmer, in press) that *S. b. beldingi* do not reach maximum body size until late in their second year of life or beyond. Likewise, Sheppard (1972) found that yearling *S. richardsonii* aged on the bases of eye lens weight, tooth wear, and epiphyseal closure had smaller mean body weights than older animals.

The habitual lack of a reproductive cycle among certain male members of a population could not be tolerated unless a mating system were employed that assured impregnation of all receptive females. A priori one might expect reproductively active males in such a system to be polygamous. The details of the mating system of *S. b. beldingi* should be elucidated shortly by behavioral studies in progress at Tioga Pass by Paul Sherman of the University of Michigan.

The social system of a ground squirrel population has recently been implicated in sexual development of yearling males. Slade and Balph (1974) found that yearling male *S. armatus* seldom had scrotal testes and rarely, if ever, bred. After the population was artificially reduced, however, many yearling males were sexually active. Slade and Balph associate this precocity with low harassment as juveniles, early arousal from hibernation, and decreased encounters with aggressive squirrels following emergence. They did not report on body size in these animals.

It is possible but improbable that we have been studying a ground squirrel population with unique growth patterns and mating system. It is important to recognize that accurate aging in many studies has not been possible due to their brevity or to lack of history on recognizable individuals. For example, in his study of *S. b. oregonus* conducted in Lassen County, California, at 1,370 to 1,730 m elevation, McKeever (1963) refers only to adults and juveniles. Body weights shown for adult *S. b. oregonus* are 5 to 10 percent lower throughout the season than those of *S. b. beldingi* (Morton 1975), but juvenile *S. b. oregonus* are at least

20 percent heavier than *S. b. beldingi* (Morton, Maxwell, and Wade 1974) before entering hibernation. Mean maximum testicular weight occurs in both subspecies at the beginning of the active season, but it is about three times greater in *S. b. beldingi* than in *S. b. oregonus*. This seems anomalous to us and, coupled with body weight data and McKeever's observation that only 70 percent of adult male *S. b. oregonus* were sexually active, suggests that at least some yearling *S. b. oregonus* could be distinguished from older animals on the bases of body size or reproductive capacity if ages were known.

Finally, it should be recognized that unusual ecological conditions exist at high altitude. Many factors, both terrestrial and extraterrestrial in origin, could function as inhibitors of growth and development in young animals.

Seasonal breeding.— Growth of the reproductive tract during the whole hibernation period is well known among *Spermophilus*. Remarkably, gonadal recrudescence, at least of testes, begins even prior to dormancy in several species with short active seasons such as *S. undulatus* (Mitchell 1959; Hock 1960), *S. b. oregonus* (McKeever 1963), *S. lateralis* (McKeever 1964), *S. richardsonii* (Clark 1970), and *S. b. beldingi* (present study). McKeever (1963) noted that *S. b. oregonus* emerged with testes of maximum size. Usually the final stages of spermatogenesis in hibernatory *Spermophilus* are not reached until ten days or more after emergence even in species at high latitude (Hock 1960). The total readiness of *S. b. beldingi* to reproduce at time of emergence is undoubtedly a response to conditions imposed by the short summers of high altitude.

Seasonal breeding is highly adaptive in that young are born at a time favorable for their survival. At high altitude this favorable season is compressed temporally and has rather sharply drawn boundaries. To cope successfully with these circumstances the cycle of sexual maturation in *S. b. beldingi* is completed during dormancy. A corollary is that reproductive preparation must have a precise phase relationship to average snowmelt patterns and related environmental effects. There is sensitivity, however, on the part of newly emerged animals to ambient conditions. At Tioga Pass considerable annual variation in snowpack, schedule of snowmelt, and emergence of vegetation were documented (Morton, Maxwell, and Wade 1974; Morton, in press). The schedule of *S. b. beldingi* was affected accordingly. In 1969, for example, snowpack was about 240 percent above normal, whereas in 1972 it was 35 percent below normal. As judged by subsequent emergence times of juveniles and their growth curves, reproduction occurred about three weeks later in 1969 than in 1972 (Morton, Maxwell, and Wade 1974). Reproduction is not delayed inordinately, however, even in heavy snow years, because about 25 percent of prehibernatory fat reserves still remain at emergence, providing a buffer to food requirements during the first weeks of activity (Morton 1975).

Acknowledgments.— Many Occidental College students participated in portions of this study. We are grateful to all of them but would like to acknowledge in particular Phil Bekey, Cassie Cusick, Shena Huang, Roland Leong, Cathy Maxwell, Robert Parmer, and Charlie Wade. Financial support was provided by Occidental College and by National Science Foundation Grant GB 29146X1.

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A NEW COMBINATION IN *PENSTEMON* (SCROPHULARIACEAE)

Stephen L. Clark[1]

Abstract.— Field and herbarium studies of Penstemon cyananthus Hook. ssp. longiflorus Pennell suggest that this taxon be elevated to species rank.

Penstemon cyananthus Hook. ssp. *longiflorus* Pennell is a tall, attractive blue-flowered plant presently known only from Beaver, Millard, and Piute counties of southern Utah. It was first collected by Edward Palmer (376, NY) near Beaver City, Utah, and was distributed as *P. glaber cyananthus*, a synonym of *P. cyananthus.*

Pennell recognized that Palmer's collection differed from the species as follows: the calyx lobes are broader than in the species, the flowers longer, the stems and lower leaves are puberulent, and the inflorescence is strongly secund. In addition, the distributions are very different. *Penstemon cyananthus* ssp. *cyananthus* has never been collected from southern Utah, but it is one of the most frequenty encountered species of *Penstemon* in the Wasatch mountains of northern Utah, southeastern Idaho, and southwest Wyoming (Fig. 1).

On the basis of these morphological and geographical differences, Pennell (1920) described and named the subspecies *P. cyananthus* ssp. *longiflorus.*

It is the writer's opinion that differences of such magnitude warrant the elevation of this taxon to specific status, hence the following new combination is proposed:

Penstemon longiflorus (Pennell) Clark comb. nov., based on *P. cyananthus* Hook. ssp. *longiflorus* Pennell in Contr. from the U.S. Nat. Herb., vol. 20, part 9, p. 353, 1920.

Penstemon longiflorus can easily be recognized by its puberulent lower stem and leaves, broad sepals, longer corolla, secund inflorescence, and its blue tipped staminode.

Both taxa have a chromosome number of 2n = 16.

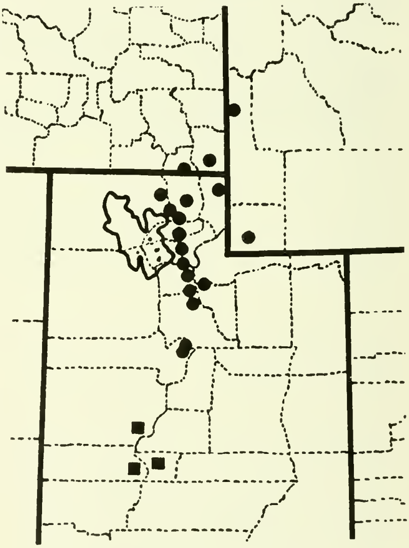

Fig. 1. Distribution of *P. cyananthus* (circles) and *P. longiflorus* (squares).

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SOME RELATIONSHIPS BETWEEN WATER FERTILITY AND EGG PRODUCTION IN BROWN TROUT (*SALMO TRUTTA*) FROM MONTANA STREAMS

Lawrence L. Lockard[1]

Abstract.— Relationships between water fertility (as measured by conductivity and alkalinity) of 17 Montana streams and the attainment of sexual maturity and fecundity of their resident female brown trout were studied. Fish from the streams having conductivity and alkalinity levels greater than 100 micromhos/cm and ppm $CaCO_3$, respectively, were younger at sexual maturity than fish from waters with lower levels. The attainment of earlier sexual maturity in fish from the former streams could not be completely explained on the basis of greater growth rates. Fish from the stream having the highest levels of conductivity had the slowest growth rate but became sexually mature at the youngest age. A positive relationship was found between chemical fertility of streams and the fecundity of their fish. However, in the stream having the highest levels of conductivity, fish were the least fecund. It was concluded that the chemical fertility of these streams is generally related to the age at sexual maturity and fecundity of fish.

The size and age at sexual maturity and the fecundity of female fish appear to be related to features of their environment. In Pennsylvania brown trout (*Salmo trutta*) from infertile waters had a smaller proportion of mature fish per age class and smaller weight of eggs than comparable fish from fertile waters (McFadden, Cooper, and Anderson 1965). Scott (1962) and Bagenal (1969) demonstrated that rainbow trout (*Salmo gairdneri*) and brown trout, respectively, brought a lower number of eggs to maturity under reduced nutritional levels than fish on higher levels of nutrition.

This study is an attempt to determine the relationships between the conductivities and alkalinities of Montana streams and (1) the size and age at sexual maturity and (2) the fecundity of the brown trout in those streams. Field collections were made from 8 September to 23 October 1972 and from 1 September to 19 October 1973.

Methods

A total of 449 female brown trout were collected by electrofishing at sites on streams in the Clark Fork of the Columbia River and in the Yellowstone and Missouri River drainages (Fig. 1). These streams had a wide range of physical and chemical conditions (Table 1).

At least one fall, winter, and summer measurement of conductivity and alkalinity was made at each collecting site. The field measurements from each stream were averaged with the yearly conductivity and alkalinity averages obtained from Water Resources Data for Montana (U.S.G.S. 1972) where available. Discharge values were obtained by averaging available yearly values from the above U.S.G.S. records with values measured or estimated by fisheries biologists of the Montana Fish and Game Department.

All fish were collected during September and October of 1972 and 1973 (Table 2). Fish taken were preserved in 10 percent formalin and later washed in water and stored in 40 percent isopropyl alcohol. Fixation in formalin causes specimens to shrink about 3-4 percent in length and increase 5-12 percent in weight (Parker 1963). After preservation, fish were measured, weighed, and scale samples were removed for age determinations. Each fish was classified as mature or immature according to the condition of the eggs in its ovaries. Mature fish containing eggs in a gradient of sizes were not used in the fecundity analyses because the number of eggs is reduced by resorption throughout the maturation period, and regressing eggs could not be distinguished from maturing eggs in these fish. Only fish having distinct recruitment and maturing eggs without intervening size classes of eggs were used in fecundity work. The ovaries from these fish were removed and the number of maturing eggs determined by actual count.

The streams from which collections

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[1] Current address: 312 South Grant Avenue, Pierre, SD 57501.

TABLE 1. Selected chemical and physical features of streams sampled.

Collection site no.[1]	Location of site	Conductivity (micromhos/cm)	Alkalinity (ppm $CaCO_3$)	Discharge (C.F.S.)
1	Rock Cr.	70	49	169
2	St. Regis R.	80	51	555
3	Big Hole R.	207	117	1,125
4	W. Gallatin R.	230	118	791
5	Madison R.	249	107	1,409
6	Baker Cr.	317	154	70
7	O'Dell Cr.	348	167	100
8	L. Prickley Pear Cr.	358	195	69
9	E. Gallatin R.	360	195	400
10	Shields R.	402	221	159
11	Flagstaff Cr.	405	197	5
12	Beaverhead R.	521	193	405
13	16 Mile Cr.	522	195	50
14	So. F. Musselshell R.	561	243	83
15	Little Blackfoot R.	612	188	105
16	Bluewater Cr.[2]	798	209	18
17	Big Horn R.	805	188	3,500
18	Bluewater Cr.[3]	1,387	214	28

[1] See Figure 1

[2] Section above Bluewater Fish Hatchery

[3] Section below Bluewater Fish Hatchery

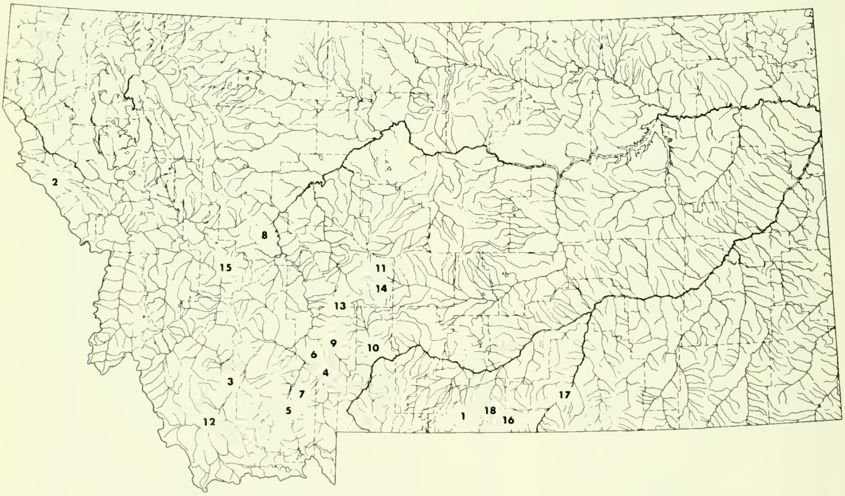

Fig. 1. Map showing location of collecting sites.

were made were grouped into classes primarily on the basis of similarities in conductivities following the technique used by McFadden et al. (1965). Streams from which collections 1 and 2 were taken each had less than 100 units of conductivity and alkalinity and formed Class I. Streams from which collecting sites 3 through 18 were located had alkalinity values above 100; thus conductivities were used as the primary indicator of water fertility. Class II contained streams on which collection sites 3 through 11 were located. These streams had conductivities ranging from 207-405 micromhos/cm at 25 C. Streams of collecting sites 12 through 15 had conductivities of from 521-612 and comprised Class III except for the analysis of size and age at sexual maturity in which Stream 17 was includ-

TABLE 2. The location, date, and number of fish collected.

Collection site	1972 Collection date	1972 Number fish	1973 Collection date	1973 Number fish	Total fish
1 (Rock Cr.)	Oct. 13	16	Sept. 14	17	33
2 (St. Regis R.)	....	....	Sept. 1	22	22
3 (Big Hole R.)	Oct. 9	17	....	....	17
4 (W. Gallatin R.)	Oct. 18	17	Sept. 25	11	28
5 (Madison R.)	Sept. 21	13	Sept. 20	19	32
6 (Baker Cr.)	Oct. 10	17	Sept. 26	9	26
7 (O'Dell Cr.)	Sept. 22	11	Sept. 21	8	19
8 (L. Prickley Pear Cr.)	Oct. 23	16	Oct. 2	17	33
9 (E. Gallatin R.)	Sept. 18	15	Oct. 4	16	31
10 (Shields R.)	Oct. 6	11	Sept. 24	6	17
11 (Flagstaff Cr.)	Oct. 9	9	....	....	9
12 (Beaverhead R.)	Sept. 26	14	Oct. 17	9	23
13 (16 Mile Cr.)	Sept. 11	13	Oct. 11	14	27
14 (So. F. Musselshell R.)	....	....	Sept. 24	13	13
15 (Little Blackfoot R.)	....	....	Oct. 1	28	28
16 (Bluewater Cr.)[1]	Sept. 8	13	Sept. 12	14	27
17 (Big Horn R.)	....	....	Sept. 15	14	14
18 (Bluewater Cr.)[2]	Sept. 8	13	Sept. 12	37	50

[1] Section above Bluewater Fish Hatchery
[2] Section below Bulewater Fish Hatchery

ed. The streams of Class II and III were combined into Class IV because their fish had similar relationships to conductivity. Class V was made up of Bluewater Creek on which collecting sites 16 and 18 were located. These collecting sites were grouped together primarily because of their high conductivities.

The fish in stream classes were statistically compared by selected procedures and techniques from "Statistical Methods" (Snedecor and Cochran 1971) and "Statistical Methods" (Arkin and Colton 1972). Additional techniques were provided by Dr. R. E. Lund, Mathematics Department, Montana State University.

RESULTS

Size and Age of Sexually Mature Female Brown Trout

Generally the attainment of sexual maturity of fish is dependent on size and age. Inspection of age groups within stream classes indicated an apparent tendency for a higher proportion of the larger females to be sexually mature (Table 3). To test the linearity of this trend, regressions were made on fish from age groups in stream classes showing an increase in sexual maturity with increasing length. In age group I, fish from Class V streams showed a significant positive linear relationship between length and sexual maturity ($P = 0.001$). In age group II, a significantly higher proportion of larger fish were sexually mature in Stream Classes I, II, III, and IV with P values of less than 0.05. In age group III^{+}, fish from Stream Classes II and IV had significant positive linear relationships between length and sexual maturity ($P<0.05$). McFadden et al. (1965) found a tendency within a given year class for a higher percentage of larger than smaller fish to be sexually mature.

The effect of age on the attainment of sexual maturity in fish was determined by comparing the proportions of sexually mature fish between age groups by a technique of R. E. Lund. Only 2 percent of age group I fish 8.0-13.9 inches long from Class IV streams were mature, while 34 percent of comparably sized fish in age group II were mature. The difference in proportions was significant with a $P = 0.001$. There were significantly fewer mature 6.0-8.9 inch fish from Class V streams in age group I than in age group II ($P = 0.08$). These combined probability values demonstrated a significantly ($P = 0.001$) higher proportion of age II fish were mature than age I fish. Significantly more of size group 10.0-19.9 inch fish from Class IV streams were mature at age III^{+} than age II ($P = 0.001$). This relationship of a higher percentage of older females being sexually mature than younger females in the same size group has been reported by McFadden et al. (1965).

Table 3. Size and age of sexually mature female brown trout by stream classes.

Age group	Length (inches)	Stream classes									
		I		II		III		IV		V	
		#Fish	%Mat.	#Fish	%Mat.	#Fish	%Mat.	#Fish	%Mat.	#Fish	%Mat.
I											
	4.0-4.9	0	....	0	....	0	....	0	....	5	0
	5.0-5.9	0	....	0	....	0	....	0	....	3	33
	6.0-6.9	3	0	0	....	0	....	0	....	16	31
	7.0-7.9	4	0	1	0	0	....	1	0	17	47
	8.0-8.9	1	0	7	0	2	0	9	0	6	100
	9.0-9.9	1	0	6	0	5	0	11	0	0	....
	10.0-10.9	0	....	11	0	10	0	21	0	0	....
	11.0-11.9	0	....	0	....	7	0	7	0	0	....
	12.0-12.9	0	....	0	....	2	0	2	0	0	....
	13.0-13.9	0	....	0	....	2	50	2	50	0	....
	Total	9	0	25	0	28	4	53	2	47	43
II											
	6.0-6.9	0	....	0	....	0	....	0	....	1	100
	7.0-7.9	0	....	0	....	0	....	0	....	6	67
	8.0-8.9	2	0	1	0	0	....	1	0	6	83
	9.0-9.9	9	33	5	0	2	0	7	0	5	100
	10.0-10.9	6	33	16	13	9	11	25	12	1	100
	11.0-11.9	1	100	29	31	3	0	32	28	1	100
	12.0-12.9	2	100	23	61	9	22	32	50	4	100
	13.0-13.9	1	100	9	67	7	57	16	63	0	....
	14.0-14.9	0	....	19	84	3	100	22	86	0	....
	15.0-15.9	0	....	3	67	5	80	8	75	0	....
	16.0-16.9	0	....	1	100	4	100	5	100	0	....
	17.0-17.9	0	....	1	100	3	100	4	100	0	....
	18.0-18.9	0	....	0	....	2	100	2	100	0	....
	19.0-19.9	0	....	0	....	1	100	1	100	0	....
	Total	21	43	107	48	48	50	155	48	24	88
III+											
	8.0-8.9	0	....	0	....	0	....	0	....	1	100
	9.0-9.9	0	....	0	....	0	....	0	....	1	100
	10.0-10.9	3	67	1	0	0	....	1	0	0	....
	11.0-11.9	8	75	3	67	1	100	4	75	2	100
	12.0-12.9	1	100	4	100	2	100	6	100	0	....
	13.0-13.9	5	100	12	92	6	100	18	94	0	....
	14.0-14.9	2	50	13	92	4	75	17	88	1	100
	15.0-15.9	2	100	16	100	9	100	25	100	1	100
	16.0-16.9	2	100	14	93	1	100	15	93	0	....
	17.0-17.9	1	100	8	100	2	100	10	100	0	....
	18.0-18.9	1	100	5	100	3	100	8	100	0	....
	19.0-19.9	0	....	3	100	1	100	4	100	0	....
	20.0-20.9	0	....	1	100	0	....	1	100	0	....
	Total	25	84	80	94	29	97	109	95	6	100
Grand Total		55	55	212	59	105	51	317	57	77	61

Comparisons were made of the proportions of sexually mature female brown trout between stream classes using a method of Arkin and Colton (1972). No significant difference (0.05 level) was found in the proportion of mature females in Class II and III streams either by age group or grand total so further comparisons by this method were made between the fish of Stream Classes I, IV, and V.

There was no significant difference between Class I and IV streams in the proportions of mature females in age group II; however, Class IV streams had a significantly higher proportion of mature females in age group III+ than did Class I streams (P = 0.054). Class V streams had a higher proportion of sexually mature females than both Class I and IV streams in both age group I (P = 0.014 and 0.001, respectively) and age group II (P = 0.001 and 0.001, respectively).

Fisher's randomization test (Bradley 1968) was used to further test the hypothesis that maturation increases as conductivity increases. The probability of obtaining the increased proportions of mature fish in all age groups with the increasing conductivities in Stream Classes I, II, III, and V (Table 3) is P= 0.00014.

The class I and IV streams in this study were similar in conductivity and alkalinity to the infertile and fertile streams in the studies of McFadden and Cooper (1962) and McFadden et al. (1965). In the latter study, fish from fertile waters attained maturity at an earlier age than those from infertile waters. This was attributed partially to a greater growth rate of fish in fertile waters; however, the authors also found higher proportions of fish of the same size and age were sexually mature in fertile streams.

In the present study, this latter relationship was not observed among fish from Class I and IV streams. Instead, higher proportions of females of a given size and age tended to be mature in the less fertile Class I streams. The differences in age at maturity between fish from Stream Classes I and IV, therefore, seem closely related to differences in growth rate. The distribution of sizes of specimens of given age groups do indicate faster growth rates in Class IV streams (Table 3). McFadden and Cooper (1962) also reported positive correlations between growth rates of brown trout and environmental fertility.

Class V streams had higher conductivity and alkalinity values than any of the streams studied by McFadden et al. (1965). In the more fertile waters (Class V), fish matured at younger ages than in less fertile waters (Classes I through IV); however, this early maturity in Class V streams was not due to a faster growth rate in fertile waters. That is, the smallest fish in each age group are found in the Class V streams (Table 3). Therefore, some factor other than growth rate or chronological age apparently influenced the size and age at which sexual maturity was reached by fish from the very fertile (chemically) waters of Class V.

Fecundity

Regression analyses for the number of mature eggs in a fish (dependent variable) on fish length (independent variable) were applied to the fish of the individual streams and stream classifications. T tests for the regression of numbers of eggs on lengths were statistically significant at the 0.05 level for fish from all streams and stream classifications with most probability values being less than 0.01. Flagstaff Creek and the Big Horn River were omitted from analyses because of an insufficient number of mature fish.

The regression lines of numbers of eggs regressed on fish length in stream classifications are shown in Figure 2. The regression lines with steeper slopes show a greater increase in number of eggs per increment of length than lines with lesser slopes.

Regression coefficients, slopes of the regression lines, were calculated for these regressions on each stream and stream classification (Table 4). The slopes of the stream classification regressions were tested for significant differences by a method of R. E. Lund (Table 5). Six of the 8 comparisons of slopes of regressions were significantly different at the 0.05 level.

Fish from Stream Class I were less fecund than fish from Stream Class II (Fig. 2 and Table 4). The difference between these stream classes was statistically significant at the 0.05 level (Table 5). This relationship of increased fecundity with increased conductivity is similar to that

Table 4. Regression coefficients (slopes) of streams and stream classifications.

Stream or classification	No. of eggs regressed on fish length		
	Regression coefficient	Std error	N
Rock Cr.	213	22	18
St. Regis R.	173	47	12
Stream Class I	254	22	30
Big Hole R.	284	40	7
W. Gallatin R.	426	83	14
Madison R.	457	64	16
Baker Cr.	164	53	13
O'Dell Cr.	248	51	14
L. Prickley Pear Cr.	236	43	16
E. Gallatin R.	218	29	19
Shields R.	252	43	16
Stream Class II	325	20	115
Beaverhead R.	172	98	15
16 Mile Cr.	143	48	15
So. F. Musselshell R.	315	112	6
Little Blackfoot R.	249	65	15
Stream Class III	286	39	51
Stream Class IV	318	18	166
Bluewater Cr.[1]	170	20	19
Bluewater Cr.[2]	113	16	21
Stream Class V	147	13	40

[1] Section above Bluewater Fish Hatchery
[2] Section below Bluewater Fish Hatchery

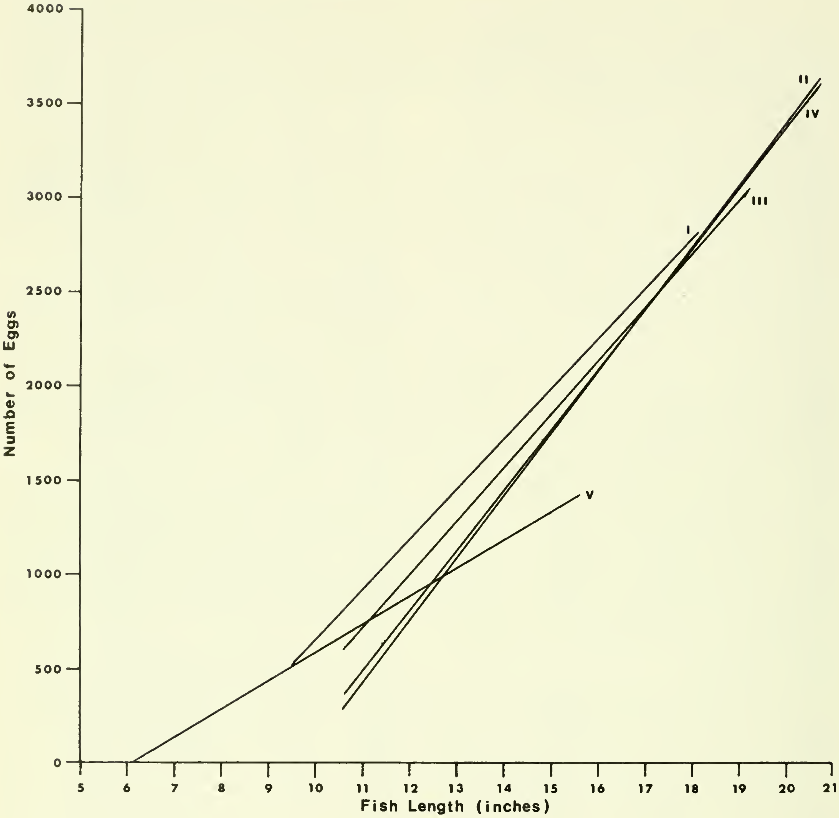

Fig. 2. The regression lines of number of eggs on length for fish in stream classifications.

Table 5. Comparisons between stream classes by slopes of regressions of number of eggs on fish length.

Slope comparison	Number of eggs regressed on fish length		
	T	df	P
I vs II	2.42	77	0.018*
I vs III	0.72	46	0.475
I vs IV	2.25	73	0.028*
I vs V	4.18	47	0.000*
II vs III	0.90	75	0.371
II vs V	7.61	149	0.000*
III vs V	3.39	60	0.001*
IV vs V	7.80	174	0.000*

*Significant at the 0.05 level

found by McFadden et al. (1965) in fish from infertile and fertile streams having conductivities and alkalinities similar to those of Class I and II streams in this study.

Fish from Stream Class III appeared to be more fecund than fish from Stream Class I (Fig. 2 and Table 4). This relationship of increased fecundity with increased conductivity was not statistically significant at the 0.05 level (Table 5). Stream Class III contained streams with higher levels of conductivity than those reported by McFadden et al. (1965).

Fish from Stream Class IV (Stream Classes II and III combined) represent fish from a broad category of chemically fertile streams with conductivities from about 200 to 600 micromhos/cm. In general, these fish were more fecund (P=

0.028) than fish from Class I streams, which represent chemically infertile waters.

Fish from Stream Class V, which had the highest conductivity, had the lowest fecundity. The conductivity values of this stream were about three times greater than the highest values reported by McFadden and Cooper (1962). The above results suggest some factor other than conductivity is determining the fecundity of fish in this stream class.

Summary

An inverse relationship between chemical fertility and age at sexual maturity was found in brown trout from streams of Montana in this study. This same relationship between the chemical fertility of streams, as measured by conductivities and alkalinities, and the age of sexual maturity of brown trout from Pennsylvania has been reported by McFadden et al. (1965). They suggested this relationship was due partially to fish in fertile streams having greater growth rates. Growth rate may account for the age at maturity in fish from 16 of the 17 streams in this study, but cannot explain the age at maturity in fish from Bluewater Creek. Fish from Bluewater Creek attained sexual maturity much earlier than fish from less fertile streams; however, these fish from the stream with the highest conductivity had the poorest growth rates of all the fish studied. This shows growth rate was not the determining factor in the attainment of sexual maturity for fish from Bluewater Creek.

McFadden et al. (1965) found a positive relationship between the chemical fertility of streams and the fecundity of their fish. A similar relationship was found between chemical fertility and fecundity in fish of this study from streams having conductivities similar to those studied by McFadden et al. (1965). However, fish from Bluewater Creek, chemically the most fertile stream, were the least fecund. Generally the age at sexual maturity of fish from all stream classes and the fecundity of fish from Stream Classes I, II, III and IV appeared to be related to the chemical fertility of their streams.

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SOME RELATIONSHIPS BETWEEN INTERNAL PARASITES AND BROWN TROUT FROM MONTANA STREAMS

Lawrence L. Lockard[1], R. Randall Parsons[1], and Barry M. Schaplow[1]

Abstract.— Forty-five percent of 306 brown trout from 16 Montana streams were infected with one or more of the nematodes *Cystidicoloides salvelini, Bulbodacnitis globosa, Rhabdochona* sp., and *Eustrongylides* sp. The relationships between incidence and intensity of nematode infections and age and sexual maturity of the host fish were studied. Generally, sexually mature female brown trout had a higher rate of infection and had more nematodes per infected fish than immature female brown trout. Higher incidence and intensity of infection in sexually mature fish was attributed to more aggressive feeding behavior leading to more exposure to the intermediate hosts (mayflies) of the nematode parasites.

Numerous parasitological surveys of trout in North America have been reported; however, few have included information on the parasites of brown trout (*salmo trutta*). Van Cleave and Mueller (1934) studied 13 brown trout from Oneida Lake, New York, and 3 from one of its tributary streams. Fifty-eight Wisconsin brown trout were studied by Bangham (1946) and Fischthal (1947a, 1947b, 1950, and 1952), with 54 originating from streams. In the western geographic region of the United States the studies of Bangham (1951), Hugghins (1959), Alexander (1961), and Fox (1962) include information on the parasites of brown trout. In these studies a total of 55 brown trout were examined: 51 from lakes and 4 from streams. Heckmann (1971) examined 28 brown trout from Montana for blood parasitism.

This study is an attempt to examine some relationships between internal parasites, brown trout, and the fish's stream habitat. It is based on the necropsy of 306 brown trout collected from 17 sites on 16 streams in south and western Montana. The specimens were collected in early September through October (1972 and 1973) just prior to and during the spawning seasons. According to Van Cleave and Mueller (1934), fish are most heavily parasitized in the summer season when they are most actively feeding. Since Fox (1962) found nematode infections in Montana brown and rainbow trout (*Salmo gairdneri*) highest in August and September. these findings may be indicative of near maximum parasite infections for brown trout in Montana streams.

Methods and Materials

All fish were collected by use of electrofishing gear described by Vincent (1967). Collecting sites were selected to reflect a wide range of geographic locations (Fig. 1), and physical and chemical conditions (Table 1). Collections were taken on both sides of the Continental Divide from streams belonging to the Clark Fork of the Columbia, Yellowstone, and Missouri River drainages. At least one fall, winter, and summer measurement of conductivity and alkalinity was made on each stream. These field measurements were averaged with the available yearly conductivity and alkalinity averages obtained from Water Resources Data for Montana (USGS 1972). Discharge values were obtained by averaging available yearly values from the above USGS records with values measured or estimated by fisheries biologists of the Montana Department of Fish and Game. The streams sampled varied in average discharge from 5 cubic feet per second to 1,409 cubic feet per second, in average conductivity from 70 to 1,387 micromhos /cm at 25 C., and in alkalinity from 49 to 221 ppm $CaCO_3$. Ecologically the streams are diverse although they all support naturally reproducing populations of brown trout.

Immediately after capture the fish were preserved in 10 percent formalin, washed in water and stored in 40 percent isopropyl alcohol for later examination. Parker (1963) indicates fish shrink about 3-4 percent in length and gain between 5 and 12 percent in weight when preserved in formalin. About three to eight months after collection fish were individually

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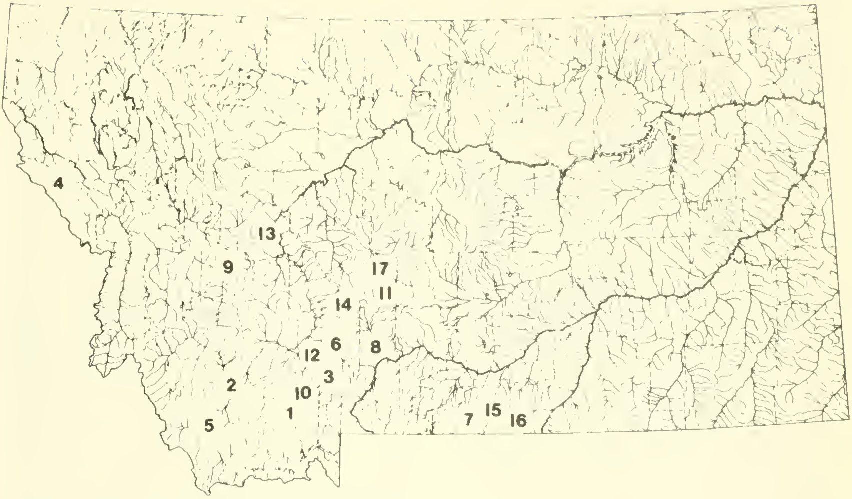

Fig. 1. Map showing location of collecting sites.

TABLE 1. Selected physical and chemical characteristics of 16 Montana streams and the incidence and intensity of nematode infections in brown trout from them.

Collection site no.[1]	Stream	Stream dis-charge	Cond.	Alk.	# Fish	% Par.	Ave. # worms par./fish
1	Madison R.	1409	249	107	13	100	68.7
2	Big Hole R.	1125	207	117	19	100	14.3
3	W. Gallatin R.	791	230	118	17	100	21.7
4	St. Regis R.	555	80	51	22	14	1.7
5	Beaverhead R.	405	521	193	14	43	1.7
6	E. Gallatin R.	400*	360	195	15	87	3.9
7	Rock Cr.	169	70	49	16	63	3.4
8	Shields R.	159	402	221	11	18	1.5
9	L. Blackfoot R.	105	612	188	28	21	1.2
10	O'Dell Cr.	100*	348	167	11	46	3.0
11	So. F. Musselshell R.	83	561	243	13	8	1.0
12	Baker Cr.	70*	317	154	28	39	1.9
13	L. Prickley Pear Cr.	69	358	195	21	5	1.0
14	16 Mile Cr.	50*	522	195	13	0	0
15	Bluewater Cr.[2]	28	1387	214	27	56	2.1
16	Bluewater Cr.[3]	18	798	209	22	77	3.7
17	Flagstaff Cr.	5*	405	197	16	0	0

*Estimated by fisheries biologists of the Montana Department of Fish and Game.

[1] See Figure 1

[2] Section below Bluewater Fish Hatchery

[3] Section above Bluewater Fish Hatchery

measured and weighed, and scale samples were taken for age determinations. The ovaries were removed for an unrelated fecundity study (Lockard 1974) and consequently were not included in this necropsy. Also, the heart and gas bladder were excluded because they were either mutilated or lost when the ovaries were removed. The procedure for necropsy was as follows. The gills and external body of the fish were examined for ectoparasites and fluke metacercaria, although the preserving and handling procedures greatly reduced the chances of discovering parasitic copepods, leeches, or monogenetic flukes. After removal of the remaining internal organs, the liver was dissected into small pieces, placed in a jar with water, and put on a mechanical shaker for 5-10 minutes. The contents were then washed onto a 200-mesh collecting screen and examined in an illuminated tray (Barber and Lockard 1973). The gastrointestinal tract was opened and its component parts scraped and placed with their contents in jars of water. After 5-10 minutes on the mechanical shaker, the contents of each jar were examined in the illuminated tray. The kidney and testes were examined grossly, and observed abnormalities checked microscopically. Recovered nematodes were placed in 70 percent alcohol-5 percent glycerine and later mounted in glycerine.

Results

Parasites were found throughout the upper digestive tract from the esophagus to the pyloric caeca. The examinations revealed that 45 percent of the 306 brown trout were infected with one to four genera of nematodes. Table 2 lists the occurrence of each taxon in a given stream. Identification of *Cystidicoloides salvelini*, *Bulbodacnitis globosa*, and *Rhabdochona* sp. was confirmed by Dr. James R. Adams, University of British Columbia (personal correspondence). The *Rhabdochona* sp. apparently is a new species and has been submitted to Dr. Morovec in Prague, Czechoslovakia, for further identification.

Inspection of Table 1 indicated an apparent relationship between the size of stream discharges, the percent parasitism (incidence) in fish and average number of worms per parasitized fish (intensity). Regression analyses were performed to test these relationships. The percentage of fish parasitized regressed on stream size was found to be correlated ($R^2=0.46$; T test $P=0.003$). The average number of nematodes per parasitized fish regressed on stream discharge was found to be highly correlated ($R^2=0{:}68$; T test $P=0.00004$).

The 306 fish used for this study ranged from 6.4 to 20.7 inches (16.3 to 52.6 cm) in total length and from 0.11 to 3.90 pounds (49.9 to 1769.0 grams) in weight with the mean length and weight being 12.3 inches (31.2 cm) and 0.93 pounds (421.8 grams). To test for a possible correlation between length of fish and intensity of parasitism, a regression of number of nematodes per infected fish on fish length was made on fish from the three collections with the highest percent parasitism (Table 1). Fish from each stream were tested individually to compensate for varying intensities of parasitism and differences in mean size of fish between streams. There was no significant correlation at the 0.5 level between number of parasites and length of host in fish from the Madison River, Big Hole River, and the West Gallatin River.

The relationship of fish age to the incidence and intensity of parasitism is shown in Table 3. Differences in the percent of infected fish between age classes

Table 2. Occurrence of nematode genera in brown trout from 16 Montana streams.

Collection site		*Rhabdochona*	*Bulbodacnitis*	*Cystidicoloides*	*Eustrongylides*
1	(Madison R.)	x	x	x	x
2	(Big Hole R.)	x	x	x	
3	(W. Gallatin R.)	x	x	x	
4	(St. Regis R.)	x	x		
5	(Beaverhead R.)	x	x		
6	(E. Gallatin R.)	x		x	
7	(Rock Cr.)	x		x	
8	(Shields R.)	x			
9	(L. Blackfoot R.)	x			
10	(O'Dell Cr.)	x		x	
11	(So. F. Musselshell R.)		x		
12	(Baker Cr.)	x	x	x	
13	(L. Prickley Pear Cr.)	x			
14	(16 Mile Cr.)				
15	(Bluewater Cr.)[1]	x	x		
16	(Bluewater Cr.)[2]	x	x		
17	(Flagstaff Cr.)				

[1] Section above Bluewater Fish Hatchery

[2] Section below Bluewater Fish Hatchery

TABLE 3. Incidence and intensity of parasitism in age classes of brown trout.

Age class	# Fish	% Infected	Ave. # worms/ infected fish
I	58	50	2.4
II	137	38	9.1
III+	111	52	21.3
Total (ave.)	306	(45)	(12.8)

were tested by a method of Arkin and Colton (1972) with results showing no significant differences between age classes I and II, and I and III$^+$ at the 0.05 level. Although the difference in the percent of fish infected in age classes II and III$^+$ was statistically significant ($P = 0.028$) it was not considered to be biologically significant. As the age of the fish increased the average number of worms per infected fish also increased (Table 3). These differences in the intensity of parasitism between age classes shown in Table 3 were significant at the 0.05 level.

The relationship of incidence and intensity of parasitism to age and sexual maturity in brown trout is given in Table 4. Significantly (0.05 level) more mature fish than immature fish in age classes I and II and in the overall total were infected. However, there was no significant difference between the incidence of parasitism in mature and immature fish in age class III$^+$. Mature fish in age classes II and III$^+$ and the overall total also had a significantly higher number of worms per fish than immature fish. In age class I there were no significant differences in the average number of worms in mature and immature brown trout.

Tests were made to determine the relationship of the chemical productivity of each stream with the degree of parasitism in its fish. No significant (0.05 level) correlations were found when percent parasitism and average number of worms per parasitized fish were regressed on stream conductivities and alkalinities.

In the five streams (Big Hole River, Baker Creek, Little Prickley Pear Creek, Bluewater Creek, and Flagstaff Creek) from which the 48 males were collected, there was no significant difference between their rate of infection (45.8 percent) and that of females from the same streams (48.2 percent).

DISCUSSION

Incidence of parasitism in brown trout varies with species of parasite and with habitat of the host fish. Fox (1962) found 30 brown trout from Meadow Lake, Montana, infected with fluke metacercaria of *Bolbophorus confusus*. Five of the 30 brown trout had immature stages of the nematode *Eustrogylides* sp. encysted within the body and 1 of the 30 had an unidentified nematode in its digestive tract. Van Cleave and Mueller (1934) examined 13 brown trout from Oneida Lake and 3 collected from Black Creek about one mile from its confluence with Oneida Lake, New York. The stream-inhabiting brown trout had the nematode *Cystidicoloides hardwoodi* exclusively, whereas the lake-inhabiting brown trout had the nematode *Spinitectus gracilis* and never *C. hardwoodi*. In over 1,000 fish from the lake *C. hardwoodi* was never taken; thus it was probably limited to streams.

In correlating parasitism to habitat, Van Cleave and Mueller (1934) conclude "that in fishes of wide range through a variety of environmental types, the type of parasitism is more or less closely correlated with the habitat from which the fish is taken." Bangham (1951) states "the fact that there were not many different types of habitats limited the numbers of various parasite species." Stream habitat may not favor the intermediate hosts of many lake parasites, i.e., cestodes

TABLE 4. Incidence and intensity of parasitism related to sexual maturity and age of brown trout.

Age class	# Fish	% Sex. Mat.	% Infected		Ave. # worms/ infected fish	
			Sex. mat.	Sex. imm.	Sex. mat.	Sex. imm.
I	58	19	82	43	2.1	2.5
II	137	51	47	28	11.0	5.9
III+	111	88	52	54	23.7	4.4
Total (Ave.)	306	(60)	(53)	(34)	(17.1)	(4.2)

(copepods), trematodes (snails), acanthocephalans (crustacea). Parasitic copepods and monogenetic flukes not common in streams may be favored by the lake environment. This would partially explain why nematodes were the only parasites found in these brown trout from cold water stream habitats.

Hugghins (1959) found no parasitism in four brown trout from Black Hills streams in South Dakota. Van Cleave and Mueller (1934) classified the frequency of occurrence of six species of parasites in brown trout as "occasional" based on a scale of abundant, common, occasional, and rare. Forty-one percent of 58 brown trout from Wisconsin streams and ponds were parasitized (Bangham 1946, and Fischthal 1947a, 1947b, 1950, 1952). This is comparable to the 45 percent incidence of parasitism found in this study.

The correlation of size of stream with incidence and intensity of parasitism was shown in Table 1. It can be seen from Table 2 that large streams have a greater diversity of species of nematodes than small streams. It would be expected in a large river with diverse habitat niches that the chance of intermediate and definitive hosts for a certain parasite existing together would be greater than in a smaller stream with a more restricted type of habitat.

Fox (1962) states that, in general, the longer the trout, the greater the number of individual parasites and kinds of parasites it contained. This is related to longer exposure time to parasitism, since the body length is generally determined by age. Woodbury (1940) summarized 12 previous investigations and reported that the longer fish had greater numbers of parasites in nine of these studies. Conversely, Langlois (1936) and Hubbs (1927) found shorter fish the most heavily parasitized. In this study no correlation between fish length and intensity of infection was found in fish from the three streams with 100 percent parasitism. However, the fish in these streams were not proportionately representative of all age classes; thus these results do not rule out a relationship between age and intensity of infection. This study did not show that older fish were generally more likely to be infected than younger fish (Table 3). However, it can be seen from Table 3 that as the age of the fish increases, so does the average number of worms per infected fish. This could be related to the older fish having more exposure time to parasites than the younger ones do.

The relationships of incidence and intensity of infection to feeding aggressiveness of fish as expressed by sexual maturity was examined. A higher percentage of mature fish was parasitized than immature fish in the overall total and for age classes I and II (Table 4). The difference between infection rates between mature and immature fish in the overall total could be attributed to older mature fish having more exposure time to the parasites than younger fish do. However, the differences in infection rates between mature and immature fish within age classes I and II could be the result of the fastest-growing (most-aggressive) fish in an age class reaching sexual maturity before less-aggressive fish. Bagenal (1969) fed different quantities of food to two groups of brown trout and found that the more aggressive of the under-fed fish took more than their share of the food. Consequently, the more aggressive of the starved fish had growth comparable with that of the well-fed fish. He also found that more of the better-fed fish were mature than the under-fed fish. There were no significant differences (0.05 level) between mature and immature fish in the percent infected for age class III^{+}. Nielson (1953) noted that brown trout in California began a shift in feeding habits from strictly aquatic invertebrate forms to partial diets of fish in the third year of life. An explanation for the similar percent infections for mature and immature age class III^{+} fish (Table 4) could be this change in feeding habits in which the parasite intermediate hosts (mayflies) would be preyed upon less by the larger mature fish.

McFadden, Cooper, and Anderson (1965) state that perhaps some combination of chronological age and growth rate (or the factors which determine growth rate), a "physiological age", determines the age of sexual maturity. One factor which influences growth rate and thus age at sexual maturity is the feeding aggressiveness of a fish. If sexually mature fish feed more actively than sexually immature fish, then mature fish of a given age would be larger than the immature fish in that age class and would have more exposure to parasitism through their aggressive feeding habits. The following is a comparison of mean lengths of mature and immature female brown trout within age classes. In age class I, only the Bluewater Creek collections contained mature females, and they had a mean length of 8.0 inches while the immature females from Bluewater Creek were 7.5 inches in mean length. Mature female fish from all streams of age classes II and III$^+$ had mean lengths of 13.3 and 15.1 inches, respectively; while the immature females from these age classes had mean lengths of 11.0 and 12.9 inches, respectively. Thus sexually mature fish within an age class are larger than sexually immature fish. This could be the result of more aggressive feeding habits. The most actively feeding fish would have more chances to encounter the intermediate hosts (mayflies, Hoffman 1967) of these nematode parasites (*Cystidicoloides* sp. and *Rhabdochona* sp. were 99.4 percent of all worms found) and thus more of them would be infected.

This theory to explain differences in infection rates between mature and immature fish within age classes is reinforced by inspection of the average number of worms per parasitized fish in age classes (Table 4). The mature fish in age classes II and III$^+$ and for the overall total have a higher average number of worms per fish than the immature fish. This suggests that the more actively feeding mature fish within an age class are exposed more to parasitism by their feeding habits than less actively feeding immature fish.

In age class I (Table 4) there was no significant difference (0.05 level) between mature and immature brown trout in the average number of worms per infected fish, possibly because exposure time was too short for significant differences to be expressed.

Fox (1962) found little relationship between incidence of parasitism and condition of trout. He states that possibly ". . . analysis of fecundity will show that parasite incidence does effect some host conditions." Comparison of the findings of this study with those of a fecundity study on the same fish (Lockard 1974) indicates that no general relationship between parasitism and fecundity exists. Table 1 shows the Madison and West Gallatin rivers were highly parasitized; in the above fecundity study they had the highest fecundity (steepest slopes of the regressions of number of eggs on fish length for a stream). Thus parasitism apparently did not adversely affect the fecundity of infected fish.

Acknowledgments

The authors express their appreciation to Dr. David E. Worley of Montana State University for providing laboratory space and equipment, and to Dr. William R. Gould of Montana State University and Mr. George D. Holton of the Montana Department of Fish and Game for reviewing the manuscript.

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SEXUAL DIMORPHISM IN MALPIGHIAN TUBULES OF *PTERONARCYS CALIFORNICA* NEWPORT (PLECOPTERA)

Ralph R. Hathaway[1]

Abstract.— The Malpighian tubules in female nymphs and adults of *Pteronarcys californica* Newport are larger and whiter than in males. This difference is detectable in nymphs as small as 300 mg in live weight (final instar nymphs weigh 800 to 1600 mg depending on sex), and is most pronounced in late nymphs and adults. These differences are thought to be related to the increased excretory load imposed by the synthesis of ooplasm in the late female nymph and adult.

The excretory systems of Plecoptera reflect the relatively primitive taxonomic level of this order. The Malpighian tubules are usually numerous and unbranched and have an uncomplicated relationship to the gut, joining it at the level where the midgut empties into the hindgut. Apart from this connection, the tubules are mainly free and unattached, extending throughout the body cavity. This situation is seen with textbook clarity in *Pteronarcys californica*.

Much current interest in the Malpighian tubules centers on their ultrastructure and on their function as a homeostatic organ (Berridge and Oschman 1969; Phillips and Maddrell 1974). They are involved in the elimination of salts and amines, and in water balance. Most studies have been done on terrestrial forms in which water retention and ion transport are achieved in specializations of the tubules and, at times, inclusion of tubules in the wall of the hind gut. The only studies on excretion in Plecoptera are those of Colby (1972), who used *in vivo* measurements to demonstrate the formation of a dilute urine in the aquatic nymphs of *Pteronarcys californica*. There have been no detailed morphological studies of Plecopteran Malpighian tubules.

In a study of the growth of internal organs (Branham and Hathaway 1975), I have observed that there is a distinct sexual dimorphism in the appearance of Malpighian tubules in *P. californica*, which has not to my knowledge been reported earlier.

Methods

Stoneflies were collected in the Provo River in Utah and transported alive to the laboratory. Several hundred fresh and preserved animals from all size classes were examined. The dimorphisms were generally well preserved in animals fixed in 70 percent ethanol and other killing and fixing fluids. A few animals were used for histological preparations in which 10μ sections were stained with Delafields hematoxylin. Weights of live animals were taken on an analytical balance after thorough blotting to remove excess water.

Observations

Male nymphs in the final instars weigh, on the average, about 800 mg, whereas the corresponding female nymphs are about twice as big, or 1600 mg. The Malpighian tubules in the female nymphs in all size classes above 300 mg are larger and whiter than those in the males. This difference becomes more pronounced as the animals grow larger and is at its maximum in the final instars and adults (compare Figs. 1a & c). The differences are not obvious in animals weighing less than 300 mg.

It is at about 300 mg of body weight that the body-size differences between male and female nymphs becomes discernable; therefore the onset of differences in the Malpighian tubules corresponds with this event. It is not merely size, however, that is involved in the sexual dimorphism in the Malpighian tubules. In females the tubules are boldly conspicuous because of their intense whiteness, whereas the male tubules are at first difficult to find because of their translucent, colorless or pink-tinged appearance. The female tubules, moreover, are of more uniform diameter throughout their length, while the diameter of male tubules is irregular. Females that are smaller and at least a year younger than final instar males still have tubules that are larger and whiter (compare Figs. 1a & b).

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About 20 percent of the tubules in animals of both sexes are connected anteriorly to the midgut by their distal ends (Fig. 1a). This union is formed from a delicate strand of solid connective tissue, so there is no confluence at this point be-

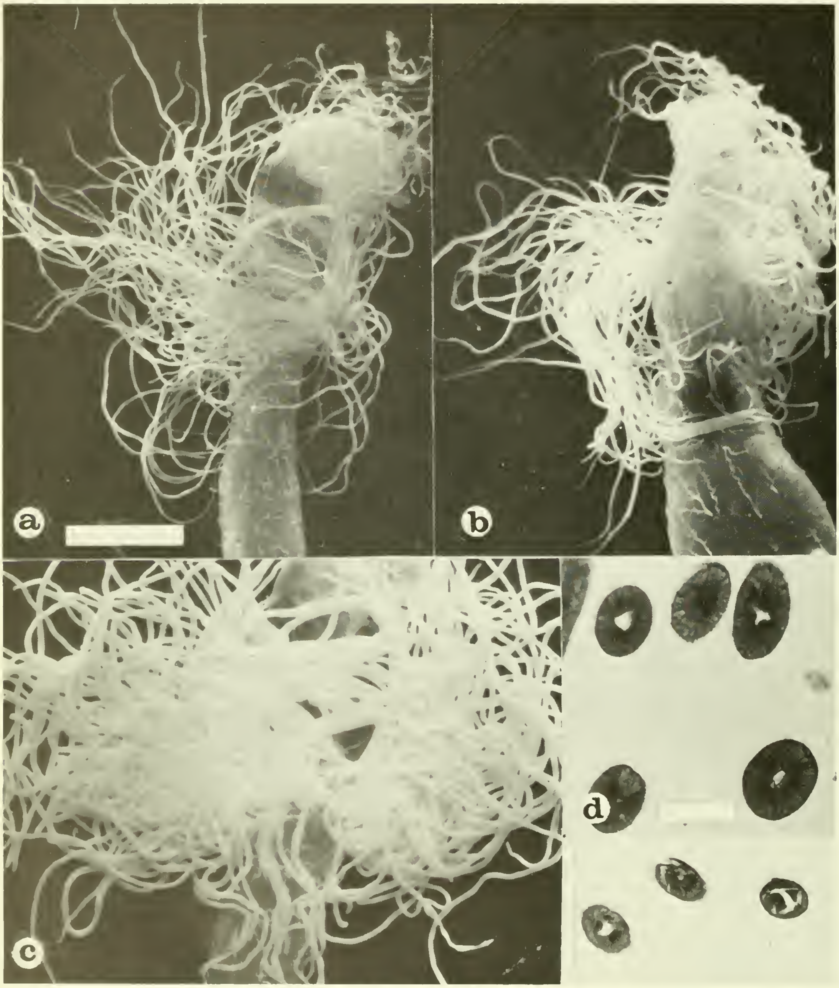

Fig. 1: Malpighian tubules in *Pteronarcys californica*: (a) Male final-year nymph. Live wt. = 840 mg. Isolated gut with anterior end down. Some of the tubules are anchored to the gut by their distal ends. Scale bar equals 2 mm. (b) Female penultimate-year nymph. Live wt. = 620 mg. Isolated gut with anterior end down. Tubules are larger and whiter than in (a). Anchored distal ends of some of the tubules are again visible. Magnification same as in (a). (c) Female final-year nymph. Live wt. = 1560 mg. Isolated gut with anterior end down. Magnification same as in (a) and (b). (d) Female final-year nymph. Cross sections of tubules. Scale bar = 0.1 mm. (e) Male final-year nymph. Cross sections of tubules. Magnification is same as in (d).

tween the lumina of the gut and the tubules. The lumina of these tubules drain into the gut at the same level as all the other tubules, i.e. at the point of junction between the midgut and the hindgut. Between their proximal and distal ends, these tubules are totally free of the gut wall; the only obvious difference from the majority of the Malpighian tubules is that their distal ends are anchored to the midgut at a point about two-thirds of the way from its anterior end, while the distal ends of the other tubules are free.

Discussion

The differences described above must have a functional basis relating to sex. Gonadal development can be seen in both sexes as they begin their final year of nymphal life. At this time males weigh about 500 mg and females weigh 900 to 1000 mg. Gonadal enlargement and sperm production are initiated early in the male; maximum gonadal size is reached midway through the final year. Corresponding events in the female do not occur until the final six or eight weeks of nymphal life. During this period a large part of metabolic effort in females is directed toward the synthesis of ooplasm. There is evidence that oogenesis utilizes substances from the fat body (Branham and Hathaway 1972). This effort continues into the adult stage, in which gamete production in the ovaries can take place for at least four weeks. Thus, one of the more obvious explanations for sexual differences in Malpighian tubules is that the redirection of metabolism associated with egg production requires more elaborate excretory organs.

Another possibility is that the Malpighian tubules in the female are involved in a secondary function such as the storage of energy-rich substances. The primary storage organ is the fat body, but this decreases in size during the time of egg production. Thus the tubules may serve to store additional reserves to be utilized during the non-feeding late-nymph and adult stages.

It seems likely that the observations recorded here have some general significance, especially in Plecoptera. Sexual dimorphism in Malpighian tubules also occurs in *Pteronarcella badia* (Pteronarcidae), which differs in many life historical respects from *P. californica*. Further observations on other species would probably be rewarding.

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NEW RECORD OF THE BAT *PLECOTUS PHYLLOTIS* FROM UTAH

Richard M. Poché[1]

Abstract.— In June 1974 a scrotal male Mexican big-eared bat (*Plecotus phyllotis*) was netted near Hurricane, Utah. This account represents the third report of the species from Utah and extends the range approximately 330 km west of previous accounts. Adjacent state records are located approximately 64 km to the southeast in Arizona and 80 km southwest in Nevada.

The Mexican big-eared bat has been reported from Utah by Black (1970) and Armstrong (1974). Both records were from San Juan County about 8 km N Blanding and 65 km NW Monticello, respectively. A specimen was reported from Pipe Springs National Monument area in Arizona by Genoways and Jones (1967), and one from the Mesquite, Nevada, region by M. J. O'Farrell (personal communication).

On 25 June 1974 a scrotal male Mexican big-eared bat was obtained in a mist net over Gould Wash, NW ¼, SW ¼, sec. 19, T. 42 S, R. 12 W, Washington Co., Utah. The locality lies approximately 7 air km southeast of the town of Hurricane. The capture of this specimen extends the range in Utah approximately 330 km to the west and represents only the third report from that state. The Arizona report is from an area about 64 km southeast of Hurricane and the Nevada account 80 km to the southwest. General similarity in habitat in the area between Hurricane and the southeastern reports suggests that *P. phyllotis* probably inhabits most of southern Utah.

The Mexican big-eared bat obtained near Hurricane, Utah, was netted over one of three small ponds remaining in the wash, striking the net approximately 1 m above the surface of the water between 0100 and 0530 hours. It was examined for ectoparasites, of which there were none, marked (with a 3 mm hole in the plagiopatagium, near the pollex, between the 4th and 5th phalanges of the right wing), and released. The bat flew west along the wash and disappeared into the canyon. Six male scrotal *Pipistrellus hesperus* also were captured in the same net and were released.

Gould Wash drains into the Virgin River 14 km northwest of the netting site. Vegetation in the wash includes *Tamarix* and *Salix*, and that on the adjacent upland is comprised primarily of blackbrush (*Coleogyne ramosissima*), and infrequent pinon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma*). Grass cover is predominantly *Bromus* and *Hilaria*. Average elevation for the area is 1,250 m with annual precipitation less than 200 mm. The Hurricane Cliffs are located 5 km west of the collection area and descend over 500 m to Warner Valley, which is covered with creosotebush (*Larrea tridentata*), blackbrush, and snakeweed (*Gutierrezia microcephala*). The surrounding region consists of numerous steep rises and mesas, canyons, and cliffs.

I thank Geoff Baillie for assistance with netting activities. David Armstrong provided helpful comments in reviewing this paper. This study was financed by the Nevada Power Company.

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